Scientific Excellence • Resource Protection & Conservation • Benefits for Canadians
Excellence scientifique • Protection et conservation des ressources • Bénéfices aux Canadiens

Migration of Northern Fur Seals (*Callorhinus ursinus*) off Western North America

Michael A. Bigg

Department of Fisheries and Oceans
Biological Sciences Branch
Pacific Biological Station
Nanaimo, British Columbia V9R 5K6

October 1990

Canadian Technical Report of Fisheries and Aquatic Sciences No. 1764

Fisheries and Oceans Pêches et Océans

Canada

91-01658/

Canadian Technical Report of
Fisheries and Aquatic Sciences No. 1764

October 1990

MIGRATION OF NORTHERN FUR SEALS (*CALLORHINUS URSINUS*) OFF WESTERN NORTH AMERICA

by

Michael A. Bigg

Department of Fisheries and Oceans
Biological Sciences Branch
Pacific Biological Station
Nanaimo, British Columbia
Canada V9R 5K6

(c)Minister of Supply and Services Canada 1990

Cat. No. Fs 97-6/1764E ISSN 0706-6457

Correct citation for this publication:

Bigg, Michael A. 1990. Migration of northern fur seals (Callorhinus ursinus) off western North America. Can. Tech. Rep. Fish. Aquat. Sci. 1764: 64 p.

ABSTRACT

Bigg, Michael A. 1990. Migration of northern fur seals (Callorhinus ursinus) off western North America. Can. Tech. Rep. Fish. Aquat. Sci. 1764: 64 p.

The annual migration of northern fur seals (Callorhinus ursinus) off western North America is described from an analysis of monthly and regional variations in the relative abundance of seals seen and collected at sea in three data sets collected during 1955-77. Three main patterns of migration are apparent. The first is undertaken by males age 1-3 yr and females age 1-2 yr. These seals remain offshore in the eastern North Pacific for much of the year with some seasonal entry in coastal regions between the Bering Sea and California. The second involves males age 4+ yr. They leave the Pribilof Islands in September-October and winter offshore in Alaska and enter coastal regions of Alaska in April-May and the Pribilof Islands in June-July. The third pattern is undertaken by females age 3+ yr. They migrate from the Pribilof Islands to the coast of California by January-February with some wintering in more northern coastal regions. The majority from California return to the Pribilof Islands by July-September using an offshore route to the Gulf of Alaska and then along the Alaskan coast. Most of the remaining seals between California and British Columbia take a direct route across the eastern North Pacific to the Aleutian Islands with others taking a coastal route. The return migration of seals up to age 4 yr is later with decreasing age and involves progressively more individuals with increasing age. Males tend to migrate before females and pregnant females before nonpregnant females of the same age. The complex migration appears related to inherited factors associated particularly with the onset of sexual maturity at age 3-5 yr and learned behaviors associated with food location.

RÉSUMÉ

Bigg, Michael A. 1990. Migration of northern fur seals (Callorhinus ursinus) off western North America. Can. Tech. Rep. Fish. Aquat. Sci. 1764: 64 p.

La migration annuelle des Otaries à fourrure (Callorhinus ursinus) à l'ouest de l'Amérique du Nord est décrite à partir de l'analyse des variations mensuelles et régionales dans l'abondance relative des otaries observées et capturées en mer, d'après trois ensembles de données recueillies entre 1955 et 1977. Trois principaux modèles de migration se manifestent. Le premier est celui des mâles âgés d'un à trois ans et des femelles d'un an ou deux. Ces otaries demeurent au large dans le nord-est du Pacifique la majeure partie de l'année, mais font quelques incursions saisonnières dans les régions côtières entre la mer de Béring et la Californie. Le second modèle est celui des mâles de quatre ans et plus. Ils quittent les îles Pribilof en septembre ou octobre, hivernent au large de l'Alaska et entrent dans les régions côtières de l'Alaska en avril ou mai et des îles Pribilof en juin ou juillet. Le troisième modèle est celui des femelles de trois ans et plus. Elles entreprennent leur migration des îles Pribilof à la côte californienne en janvier ou février en s'abritant, l'hiver, dans les régions côtières plus septentrionales. La majorité remontent de la Californie aux îles Pribilof de juillet à septembre en suivant un itinéraire au large du golfe d'Alaska puis le long de la côte de l'Alaska. La plupart des autres otaries qui restent entre la Californie et la Colombie-Britannique traversent directement le nord-est du Pacifique jusqu'aux îles Aléoutiennes alors que d'autres suivent la côte. La migration de retour des otaries âgées de quatre ans ou moins s'effectue d'autant plus tard qu'elles sont plus jeunes et réunit graduellement plus d'individus à mesure qu'elles vieillissent. Les mâles ont tendance à migrer avant les femelles et les femelles gravides avant celles du même âge qui ne le sont pas. La complexité de la migration semble reliée à des facteurs héréditaires associés principalement au développement de la maturité sexuelle entre trois et cinq ans et à des comportements acquis liés au lieu de ravitaillement.

INTRODUCTION

The northern fur seal (Callorhinus ursinus) inhabits the subarctic offshore and coastal waters of the North Pacific, Sea of Okhotsk and Bering Sea (Scheffer 1958; King 1983). The species consists of three main stocks named after the islands on which they breed (North Pacific Fur Seal Commission 1984): 1) Robben Island (northwest of Japan; 70-80,000 pups and older seals); 2) Commander Islands (western Bering Sea; 200-220,000); and 3) Pribilof Islands (eastern Bering Sea; 900,000). Three small and recently formed populations breed on the Kuril Islands (northeast of Japan; 45-50,000), San Miguel Island (California; 4,000) and Bogoslof Island (eastern Aleutian Islands; 400; Loughlin and Miller 1989). The Asian and North American stocks migrate mainly along their respective coasts.

The Pribilof Islands stock ranges from slightly north of the Pribilof Islands, along the west coast of North America to the California-Mexico border, and west to join with the offshore range of the Asian stocks (Fiscus 1986). Knowledge regarding migration of the Pribilof Islands stock is based largely on accounts by pelagic sealers of the late 1800's and by crews from United States patrol vessels (see Bissett 1890's; Hooper 1892; Townsend 1899; Ognev 1935; Zeusler 1936). Other reports include incidental observations made during the 1920's to 1952 (Kenyon and Wilke 1953) and a study undertaken off the coast from the Gulf of Alaska to California in 1952 (Taylor et al. 1955).

These accounts suggest that most of the stock migrates to the Pribilof Islands during May to October with the majority arriving in July when pupping and mating takes place. Seals migrate south from the Pribilof Islands in October-November and by November-December travel through the passes of the eastern Aleutian Islands between Unimak Pass and Amukta Pass 500 km to the west. Unimak Pass is probably the preferred route (but see Bissett 1890's). Seals then travel directly to the coast between the western Gulf of Alaska and California with most going to California. Migration is rapid because some seals begin arriving in all coastal regions by December. The favored wintering habitat is located over or near the edge of the continental shelf within 150 km of shore. A few seals remain near the Pribilof Islands and the eastern Aleutian Islands during December-April and some remain offshore all year in the eastern North Pacific.

The return migration is thought to take place more slowly. Seals in California begin their migration in March-April and move northward through the coastal waters of Oregon, Washington and British Columbia to the western Gulf of Alaska by April-June. Some remain along the coast between California and British Columbia until May. Seals then migrate west along the

Alaskan coast, through the passes of the eastern Aleutian Islands in June-July and to the Pribilof Islands. The seals rarely go ashore during their annual migration except when at the Pribilof Islands.

However, these reports provide little information on the sex- and age-specific migratory patterns of the stock, although they do indicate that migration is complex in that males tend not to travel as far south as females and that age-specific differences in migratory timing appear to exist. To improve understanding of migration and other aspects of the seals' life at sea, the governments of the United States and Canada undertook extensive studies at sea during 1958-74 as part of their research contribution to the North Pacific Fur Seal Commission. Vessels were used annually by each country to sight and collect seals along the North American coast from the Pribilof Islands to California. Results of these studies were presented by each country at annual meetings of the North Pacific Fur Seal Commission. Summaries of findings were also presented in reports of the North Pacific Fur Seal Commission (1962, 1969, 1971, 1975, 1980).

Three reports on migration were prepared from data collected by the United States and Canada during 1958-74, but none were published. Manzer et al. (1969) examined sex- and age-specific migration using data collected during 1958-67 plus sightings of northern fur seals collected in coastal and offshore areas in the eastern North Pacific by whaling and other research vessels during 1956-77. Kajimura (1980) described distribution and migration and summarized the sex and age composition of collections by region using the 1958-74 data. Bigg (1982) described migration by sex, age and reproductive condition using sighting and population composition data collected during 1958-74. In addition, French et al. (1989) published a report on migration in the eastern Bering Sea based on a simulation model which incorporated behavioral observations, data collected during 1958-74 and the reports of Kajimura (1980) and Bigg (1982).

In this study, I describe migration for the Pribilof Islands stock for seals of each sex, age and reproductive condition. The study is based largely on the data collected for the North Pacific Fur Seal Commission during 1958-74. I also analyze two unpublished data sets on the relative abundance of northern fur seals in the eastern North Pacific collected by Manzer et al. (1969). Emphasis is placed upon the migration of immature seals because the largest differences in migration exist in this age group (Taylor et al. 1955; Bigg 1986). Both males and females attain sexual maturity at typically 3-5 yr of age (Craig 1964, Bigg 1986). Thus, the study considers age-specific migration for females age 1-5+ yr (i.e., 1-≥5 yr) and males age 1-4+ yr. Also, the migration of pregnant and nonpregnant females age 5+ yr is compared.

The route and timing of migration is inferred from an analysis of monthly and regional variations in the total number of seals seen hr^{-1} and in the estimated number seen hr^{-1} of each population component. The estimated number seen hr^{-1} of each population component is determined from the sex, age and reproductive composition of seals collected. Thus, for example, an increase in the density of a particular sex and age of seals observed in a region is used to indicate movement of that population component into a region. Additional information on the migration of this stock is obtained from a review of the published and unpublished literature. The evolution of migration in the stock is discussed as is the possible role that inherent and learned behaviors may play in establishing the route and timing of migration.

METHODS

The three data sets analyzed are as follows.

1. Data from the North Pacific Fur Seal Commission

This is the largest data base. It consists of the sighting and kill data collected during 1958-74 by the United States and Canada. The study area extended along the North American coast from the Pribilof Islands to California and was divided into nine regions (Fig. 1a), seven of which have been traditionally used by the North Pacific Fur Seal Commission (see Lander 1980). Two new regions were created to more accurately describe migration. They were: 1) the Eastern Aleutian Islands, which comprised the adjoining borders between the Pribilof Islands (formerly Bering Sea region) and Western Alaska; and 2) a division of the Gulf of Alaska region into the Eastern and Western Gulf of Alaska. The outer boundaries of the nine regions extended out to about 500 km from shore in some regions and enclosed the area in which 99.0% of the seals which were collected were taken.

When considering the nine regions between Alaska and California (Fig. 1a), it is important to note that the regions are of unequal size. While I did not make quantitative comparisons involving regional sizes, I did consider relative differences in size when discussing the importance of each region to seals. Thus, a crude estimate of regional size was derived. The measure of size used for eight coastal regions was the straight-line distance from one end of a region to the other. These study regions were essentially a narrow linear strip of coastline with most data collected at a distance of 20-150 km

from shore although some data were collected out to 500 km from shore. A different measure was used for the Pribilof Islands because they are situated slightly off the Alaskan coast. The measure used here was the length of the southern latitudinal boundary plus one adjoining longitudinal boundary. The relative sizes of the regions by order of decreasing size were: California (1.0), Pribilof Islands (.8), Western Gulf of Alaska (.7), Eastern Gulf of Alaska (.7), British Columbia (.7), Eastern Aleutian Islands (.6), Oregon (.4), Western Alaska (.3) and Washington (.3).

Lander (1980) described the field and laboratory procedures used to collect the data during 1958-74. Each year both the United States and Canada used a government vessel or a chartered vessel of typically 20-30 m in length to sight and collect seals. The course taken by the vessels varied by year depending upon the research objective. Seals were sought in either a random pattern, in transects or in areas of known seal abundance. Most sampling was done within 150 km of shore. Perez and Bigg (1986, their Fig. 2) summarized the cruise tracks taken by vessels.

The total number of seals seen hr^{-1} was calculated from the number of seals seen along the cruise track as the vessel travelled at a speed of 15-19 km hr^{-1}. Seals were collected from the vessels by rifle or shotgun and examined for sex, age and reproductive condition using standard techniques. The age assignments for seals were based on the calendar year such that age changed on 1 January (Lander 1980). Thus, a seal born in July reached age 1 yr in the following January and age 2 yr in the next January. To keep age classes unified, ages were increased by 1 yr for the few seals which were collected in December. All sighting and kill data were referenced by date and location and stored on magnetic computer tape.

During 1958-74, a total of 21,600 hr of searching were logged and 18,392 seals were collected for which ages were determined. Lander (1980) listed the number of seals collected by sex, age, reproductive condition, month and region during 1958-74. The total number of seals seen hr^{-1} by month was summarized by Kajimura (1980) for 1° latitude by 1° longitude areal units and by Bigg (1982) for 1° latitude by 2° longitude areal units. A female was considered pregnant if she carried an embryo or fetus or, during June-October, was recently postpartum. Young pregnant females (<5 yr) were omitted from the study because of their small number (see Lander 1981). The 5+ yr female age group included individuals up to 26 yr. Males age 4+ yr included individuals up to 15 yr.

The number of individuals of a particular sex, age and reproductive condition seen hr^{-1} within a particular month and region was determined as follows. First, the percentage which

each population component comprised of the total number of seals collected in that month and region was calculated. These percentages were then apportioned to the total number of seals seen hr^{-1} for that month and region. Thus, the sum for the number of seals of each population component seen hr^{-1} within a month and region always equalled the total number seen hr^{-1} for that month and region.

The number of hours spent sighting seals, total number of seals seen hr^{-1} and the number seen hr^{-1} for each population component were summarized by month for all 1° latitude by 2° longitude areal units within each region of the study area. Sighting and population composition data were compared by inspection between areal units within each month and region for obvious biases, such as unusually high densities of seals or unusual population compositions. To reduce bias, data from units judged to be unrepresentative for the region as a whole were omitted from the analysis. For example, a local concentration of seals sometimes resulted in the total number seen hr^{-1} in an areal unit being clearly too high relative to other units within the region. If a relatively large number of hours of sighting was also spent in that areal unit, then an unrealistically high density of seals for that region as a whole resulted. Areal units in which unusually high densities of seals existed were (see Fig. 1a): 1) northeastern Vancouver Island (British Columbia) during January-May; 2) northern Hecate Strait (British Columbia) during February; 3) Sitka Sound (Eastern Gulf of Alaska) during February-March; 4) Albatross Bank (Western Gulf of Alaska) during April; and 5) Portlock Bank (Western Gulf of Alaska) during May-June.

However, the population composition of seals collected within these units was typical of the region as a whole and thus the population compositions within these units were used in the analysis, except for northeastern Vancouver Island and northern Hecate Strait. The population composition data from northeastern Vancouver Island (mainly Knights Inlet) were omitted because 96% of the 121 seals collected there in January-May were yearlings. An unusually high pregnancy rate (81%) for British Columbia was found in northern Hecate Strait during February.

In addition, essentially all research effort in the Eastern Aleutian Islands was undertaken in the Unimak Pass area, a site where seals tended to congregate. Thus, the total number of seals seen hr^{-1} in this region was not comparable to that of other regions. Nevertheless, the population composition data from the Eastern Aleutian Islands contributed to the understanding of migration and thus were presented in the report, although separately.

Data are not presented on the number of seals seen hr^{-1} of each population component for months in which the total number

of seals collected in a region was less than 22 (Appendix Table 1). Such sample sizes were considered to be too small to produce meaningful measures of relative abundance for each population component.

Two main assumptions were made in the analysis. The first was that the total number of seals seen hr^{-1} by month in a region was an index of the actual number present. Thus, when an increase in the number seen hr^{-1} of a particular population component took place during a month within a region, seals were assumed to have moved into that region. Similarly, differences in the number of seals seen hr^{-1} between regions would indicate differences in densities of seals between regions. In general, the assumption was likely to be valid. A research priority for the crew of each vessel was to sight and record the number and location of all seals seen along the cruise track. Sightings were made by usually 2-3 people stationed on the vessel bridge and equipped with binoculars. In addition, the migratory patterns inferred from the monthly and regional differences in densities will be shown (Results) to be in general agreement with migratory patterns described in earlier studies.

Nonetheless, the total number of seals seen hr^{-1} may still have been subject to some bias from seasonal variations in weather conditions. Thus, the density of seals reported during months of poor weather may have been underestimated relative to the density reported during months of good weather. However, this potential bias is unlikely to have seriously affected the description of annual migration. The analysis concerned seals basically either in the eastern North Pacific during winter-late spring (December-May) or approaching the breeding grounds in summer (June-September). The weather conditions for months within the two seal distributions were likely to be more similar than between the two distributions. Also, some surveys were not undertaken during days of poor weather.

The second assumption was that the population composition of seals collected by month within a region was representative of the population present. This assumption was also likely to be valid. No deliberate bias existed to collect seals of a particular sex, age and reproductive condition and seals were usually collected whenever they were sighted. However, older males (4+ yr) were probably underrepresented in collections because they were large and difficult to kill compared with other population components. This was not an important bias because males of this age were already relatively few in number from reductions by a commercial kill of males age 2-5 yr and a high natural mortality rate (see Lander 1981). Pike et al. (1960) suggested that young inexperienced seals were collected more easily than older seals. This bias would result in young seals, presumably age 1 yr or 2 yr, being overrepresented in

collections. However, few seals of these ages were taken, except for yearlings in Washington and British Columbia.

A small possibility existed that some seals sighted and collected off California originated from the newly established colony at San Miguel Island. This colony grew from a few individuals when first noted in 1954 to 100 in 1968 (Peterson et al. 1968; DeLong 1982). No sightings and no specimens were collected off California after 1966.

2. Data from research and whaling vessels

A large data set on the average number of seals seen 100 nmi^{-1} (185 km) in inshore and offshore areas of the eastern North Pacific was collected by crews aboard research vessels undertaking studies of salmon and oceanography and crews aboard commercial whaling vessels. The data were requested and compiled by J. Manzer, G. Pike and I. MacAskie of the Pacific Biological Station, Nanaimo. During 1956-66, these vessels operated in coastal and offshore areas mainly between Washington and the Western Gulf of Alaska. Manzer, Pike and MacAskie summarized the sighting data into 5° latitudinal by 5° longitudinal areal units. I divided their data into four coastal regions, which approximated the existing regions of Washington, British Columbia and the Eastern and Western Gulf of Alaska, and into four new offshore regions, each of which comprised an areal unit of 5° latitude by 10° longitude (Fig. 1b). The outer boundary of the second Washington region did not extend as far offshore as that for the 1958-74 data base. However, most effort during 1958-74 took place within the boundary of the second Washington region. In the four coastal regions, 77,214 nmi (143,093 km) of vessel travel was logged with on-station observations and in the four offshore regions 91,950 nmi (170,402 km) (Appendix Table 1). Months in which fewer than 300 nmi (556 km) were travelled within a region were considered small samples and omitted from the analysis. Although the objectives for the research and whaling vessels differed from those of the 1958-74 study and the procedures for observations were not as rigorous, this second data set provided useful information on relative abundance of seals in months and regions not adequately sampled during 1958-74.

3. Ocean Station Papa data

Manzer, Pike and MacAskie also requested and compiled data on the number of seals seen hr^{-1} by crews aboard the year-round Canadian weather station, known as Ocean Station Papa, situated offshore at 50°N latitude and 145°W longitude (Fig. 1b). During 1960-77, the crew logged 40,225 hr of observation (Appendix Table 1). I

present these data in the format in which they were summarized by Manzer, Pike and MacAskie.

RESULTS

Several points regarding the data and analyses need to be made before migration is considered by sex, age and reproductive condition. To begin the analysis, the proportion which each population component comprised in coastal collections was compared with the expected proportions for an equilibrium population, as calculated by Lander (1980, 1981). The observed proportions in all months and regions should be the same as the expected proportions if all population components migrated along the same route. However, a comparison between the observed and expected proportions indicates that six population components were underrepresented in the coastal collections (Table 1). Collected yearling males and females comprised only 41% (mean of both sexes) of the expected proportion, females and males age 2 yr were 35% of expected, males age 3 yr were 58% and males 4+ yr comprised 41% of expected. The underrepresentation of males age 1-3 yr and of females age 1-2 yr results from the fact that portions of these components inhabit mainly offshore regions. However, males age 4+ yr were underrepresented because their large body size made them more difficult to kill than other population components.

The examination of migration concerns the arrival times at wintering grounds and the route and timing of the return to the Pribilof Islands. The departure schedule of each population component from the Pribilof Islands to the wintering grounds is not well known. Very few seals remain on the Pribilof Islands by early December (Peterson 1968). Pups, females of all ages and males age 1-2 yr apparently leave at about the same time in October-November (Marine Mammal Biological Laboratory 1970; French et al. 1989; R. Gentry, National Marine Mammal Biological Laboratory, Seattle; pers. comm. 24 January 1990). Juvenile males of about age 3-4 yr leave slightly earlier and older males appear to leave earlier, perhaps by September.

Three main patterns of migration will be shown to exist. The first is undertaken principally by immature seals, many of which remain widely dispersed offshore in the eastern North Pacific all year. These seals include males age 1-3 yr and females age 1-2 yr. The second involves mature males age 4+ yr, most of which remain year-round in Alaskan waters. These two patterns of migration are described using the monthly and regional variation in the estimated number of seals seen hr^{-1} of

each sex and age based on data collected during 1958-74. The third pattern consists of maturing or mature females age 3-5+ yr. These ages likely have the same migratory route, although they migrate at slightly different times. This migratory pattern is described using the monthly and regional differences recorded in the total number of seals seen hr^{-1} and the estimated number seen hr^{-1} of females age 3, 4, 5+ pregnant and 5+ nonpregnant, based on data collected during 1958-74 and the two data sets collected by Manzer, Pike and MacAskie during 1956-66 and 1960-77. Although the monthly and regional variations in the total number of seals seen hr^{-1} (see Fig. 8) during 1958-74 will not be discussed in detail until after considering males age 1-4+ yr and females age 1-2 yr, some reference will be made to these variations when analyzing migration for males and females of the latter ages. Reference to the total number seen hr^{-1} is required because it includes the relative abundance of seals during a greater number of months than is available for each sex and age.

The study will also show that the number of individuals of each age returning and the order of departures of each age up to age 4 yr is basically the same as for arrivals on to the Pribilof Islands, as described by Bigg (1986). He showed for seals age 1-4 yr that numbers of each age returning increased with age, that males tended to return before females of the same age and that both sexes tended to return earlier with increasing age. Also, pregnant females usually returned before nonpregnant females of the same age.

MALES AND FEMALES AGE 1 YR

Some yearlings travelled rapidly from the Eastern Aleutian Islands to the coast between Western Alaska and California because they reached these regions by December (Kajimura 1979). However, relatively few individuals were seen along the coast except off Washington during January-May and British Columbia during March-May (Fig. 2; see also Fig. 8). Yearlings were also recorded in Sitka Sound in February-March (Table 2). Townsend (1899) similarly reported that a large number of yearlings was present in Washington in February. Some yearlings from Washington may have moved into British Columbia in April because numbers were still increasing in British Columbia at the same time that numbers were decreasing in Washington.

The 1-yr-olds were generally found close to shore (within 20-50 km) in Washington and British Columbia and frequently in inlets of British Columbia during January-May (Pike et al. 1958; Marine Mammal Biological Laboratory 1971). As noted in the Methods, yearlings may have been more easily collected than older seals and thus yearling densities may be inflated.

Most 1-yr-olds left the coast between the Eastern Gulf of Alaska and California by June. A small number of males reached the Eastern Aleutian Islands by June and a small number of females later in July (Table 2). A few males of this age reached the Pribilof Islands region by September, but no females returned by this time. Bigg (1986) similarly reported that yearling males arrived at the Pribilof Islands before yearling females and that a few males returned in late September-early October and a few females returned by October-early November.

Yearlings which did not reach the Bering Sea probably remained in offshore regions in the eastern North Pacific, a conclusion also reached by Manzer et al. (1969). This possibility is supported by observations of Townsend (1899) who reported that seals inhabit offshore regions all year, although not in the high densities observed along the coast. Also, a year-round presence of seals offshore was evident from the sighting observations compiled by Manzer, Pike and MacAskie at Ocean Station Papa (Fig. 3). Seals were seen during each month of the year with the largest number observed during July. These offshore observations indicate that not all seals migrate to coastal wintering regions and not all migrate to the Pribilof Islands during the summer breeding season. Presumably, some of the seals seen at Ocean Station Papa were yearlings.

Thus, when male and female pups leave the Pribilof Islands in October-November they migrate through the passes of the Eastern Aleutian Islands and probably disperse widely (Fig. 4a-b). They become yearlings in January. Some enter inshore regions of the eastern North Pacific, particularly Washington and British Columbia. However, few return to the Eastern Aleutian Islands and Pribilof Islands and those that return do so late in the summer or early fall with the vast majority presumably staying offshore mainly in the eastern North Pacific.

MALES AND FEMALES AGE 2 YR

Essentially all males and females age 2 yr were already present in the eastern North Pacific in January (Fig. 4a-b). Very few of these individuals had entered the Pribilof Islands and Eastern Aleutian Islands regions in the preceding year as yearlings. Few individuals of either sex migrated to the coast between the Western Gulf of Alaska and California (Fig. 5; see also Fig. 8). Some were present by December in Washington and by January in California. They tended to gradually move into these regions up to May, but their numbers remained small in all regions. Seals of this age appeared to move offshore in June or later. A few males moved into the Western Gulf of Alaska in July. Males arrived before females in the Eastern Aleutian Islands

(Table 2). A few males reached the Pribilof Islands region in August and small numbers of females migrated there in August-September. Bigg (1986) similarly noted that a few males age 2 yr had arrived at the Pribilof Islands in mid- to late August and that a few females age 2 yr arrived later in mid- to late September. Because relatively few seals of either sex age 2 yr entered the Pribilof Islands and Eastern Aleutian Islands regions during June-September, many of this age presumably remained in the eastern North Pacific like yearlings.

Only a small number of males (2.8%; Lander 1981) were killed in the commercial harvest on the Pribilof Islands from late June to early August. Thus, the density of males in the Pribilof Islands region at this time was comparable to other months, regions and ages. However, such comparability will not be the case for older males.

MALES AGE 3 YEARS

Most males began their third year already in the eastern North Pacific because so few returned to the Pribilof Islands as 2-yr-olds (Fig. 4a-b). During January-May, many males of this age apparently remained offshore with males and females age 1-2 yr. Small numbers arrived in Washington during December and in California during January (Fig. 6). Few were likely to be present in other coastal regions at this time (see also Fig. 8). Numbers remained small between California and British Columbia during January-June. Small numbers arrived in the Eastern Gulf of Alaska in April and were there until June. An influx into the Western Gulf of Alaska began in May and continued until at least July. Relatively large numbers arrived in Western Alaska and Eastern Aleutian Islands (Table 2) in June. Males age 3 yr had already reached the Pribilof Islands region by July. This arrival time agrees with Bigg (1986) who reported that most males age 3 yr had arrived on hauling ground on the Pribilof Islands by late July.

The density of males age 3 yr in the Pribilof Islands region during July-September was not comparable to other months, regions or ages. Commercial kills on the Pribilof Islands took an estimated 40.3% of this age group between late June and early August (Lander 1981) and thus depressed their density in the Pribilof Islands region at this time. The increase in density during September (Fig. 6) may have resulted from males of this age leaving their haulouts just prior to the southern migration.

MALES AGE 4+ YR

Adult males are thought to migrate through Unimak Pass mainly in mid-October and to spend their winter south of the Eastern Aleutian Islands and east to the Eastern Gulf of Alaska (Hooper 1892; Townsend 1899). The data collected during 1958-74 suggest a similar migration. Only a very small number of males age 4+ yr migrated south of Alaska to the coast between British Columbia and California (Fig. 6; see also Fig. 8). These males were present between British Columbia and California during January-May. However, the densities of males of this age group were probably biased too low because such males were more difficult to collect than other population components (see Methods). The return migration of this age group began with a relatively large influx into the Eastern Gulf of Alaska during April probably from offshore regions (Fig. 7a-b). Males from British Columbia, Washington and California were unlikely to have contributed to the increase seen in the Eastern Gulf of Alaska during April. Males from these regions were few in number and remained until May-June. All males which migrated to the coast between British Columbia and California were 4-6 yr of age, whereas those that remained in Alaska were 4-15 yr. Thus, with increasing age more males tended to remain in Alaskan waters.

Males from the Eastern Gulf of Alaska moved west to the Western Gulf of Alaska by May-June and Western Alaska and the Eastern Aleutian Islands by June (Table 2). Males of this age had already reached the Pribilof Islands by July. Bigg (1986) similarly reported that males of this age had reached their peak number on the Pribilof Islands mainly between late June and mid-July. As with males age 3 yr, the density of males age 4+ yr during July-September in the Pribilof Island region was depressed by a commercial kill. An estimated 57.3% of males age 4 yr and 14.7% of males age 5 yr were killed (Lander 1981). Thus, the density of males age 4+ yr in the Pribilof Islands region during July-September was not comparable to other months, regions or ages.

FEMALES AGE 3+ YR

Females age 3+ yr comprised 85.2% of all seals collected along the coast between Alaska and California (Table 1). Because essentially all hunting by pelagic sealers in the late 1800's was along the coast, their accounts of migration concerned primarily this component of the Pribilof Islands stock. Before age-specific migration is examined for females between 3 and 5+ yr of age, a description is given for the migration of all females age ≥3 yr combined because the route of migration for

these ages is probably similar. However, it will be shown that the arrival and departure times of each population component within each region took place over a shorter period of time than noted for all ages combined. A comparison of migration can thus be made between the findings using the current analysis and the findings the late 1800's.

An examination of the monthly and regional variations in the total number of seals seen hr^{-1} during 1958-74 (Fig. 8; Table 2) confirms much of the route and timing of migration described in the Introduction, although new information is also provided. The Pribilof Island seals arrived in the Washington region mainly in December, but not until about a month later (January) in California. The highest coastal density of seals in the eastern North Pacific during January-February was in California. As suggested in earlier studies, most seals migrated to California. This was indicated by the fact that the highest density occurred in California and California was the largest region.

The region with the second highest density during January-February was Washington, which had about half that recorded in California. However, relatively few seals migrated to Washington compared to California because Washington was only a small region. The density of seals was low in Oregon and British Columbia during January-February. Few seals appear to occur in the Eastern and Western Gulf of Alaska at this time although data were scarce. Seals were observed to gather in the inshore waters of Sitka Sound (Eastern Gulf of Alaska) during February-March (Table 2). Similarly, Taylor et al. (1955) recorded a local concentration of seals in Sitka Sound during January-April. However, few seals apparently inhabited the exposed areas of southeast Alaska during February-April (Wilke et al. 1958; Niggol et al. 1960). The sighting data collected by Manzer, Pike and MacAskie (Fig. 9) during 1956-66 support the view that low densities of seals occurred off the coast in the Eastern and Western Gulf of Alaska during January-February, although their sample sizes were relatively small at this time (Appendix Table 1).

Seals in California began their northern migration in March rather than March-April as indicated in earlier studies. A few seals did not leave until June or later. Most seals reached the Eastern and Western Gulf of Alaska in April-May as indicated in earlier studies. The sightings collected by Manzer, Pike and MacAskie confirm that the main arrival time of seals in the Eastern Gulf of Alaska was April-May (Fig. 9). Little can be said about the arrival time in the Western Gulf of Alaska from their data. They report a low density in the Western Gulf of Alaska during April-July compared to that in the Eastern Gulf of Alaska whereas a relatively high density was indicated from the 1958-74 data (Fig. 8). Their low density resulted from little effort

being undertaken in the more inshore areas of the Western Gulf of Alaska where seals tend to aggregate.

Seals reached Western Alaska primarily in June and the Pribilof Islands in July, as indicated in earlier studies. Seals continued to enter the Pribilof Islands region up to September. The peak density in the Pribilof Islands region may have been in October, but no sighting effort was undertaken in the region at that time. It should be noted that the density of seals in the Pribilof Islands region during June-September was underestimated because a substantial number of seals were hauled out on the Pribilof Islands at that time (see Peterson 1968; Bigg 1986; French et al. 1989).

Seals departed from the Eastern Gulf of Alaska mainly in June-July (Fig. 8-9), Western Gulf of Alaska in August and Western Alaska mainly by August-September (Fig. 8). Few seals were present along the coast from the Western Gulf of Alaska to California during September-November (Figs. 8-9), as noted in earlier studies.

Observations of migrating seals during 1958-74 confirm the findings of earlier studies that a return coastal route from California to the Pribilof Islands exists although only for some seals. Seals were observed moving northward in California waters during late March (Wilke et al. 1958) and late April (Fiscus and Kajimura 1967), northward in Oregon during mid-April (Wilke et al. 1958), northward during April in Washington (Niggol et al. 1959); and westward in Western Alaska during June (Niggol et al. 1960). However, most seals between California and British Columbia do not appear to take the coastal route to the Gulf of Alaska. Instead, seals in California apparently take an offshore path to the Gulf of Alaska whereas seals in Washington and British Columbia appear to take a direct route across the eastern North Pacific to the Eastern Aleutian Islands.

Evidence for an offshore route between California and the Gulf of Alaska comes from three sources. First, little evidence exists for an obvious migratory front moving northward through Washington and British Columbia. No increase in density of the total number seals took place in Washington and British Columbia during March-April (Fig. 8). Although a small increase in the total number seen hr^{-1} took place during March in Washington and during April in British Columbia, this increase resulted from an influx of yearlings from offshore during March-April (Fig. 2). This lack of an increase in seal density in Washington and British Columbia will be shown later more clearly with pregnant females age 5+ yr.

Also, despite considerable field effort with searches that anticipated finding the migratory front, the Canadian staff which undertook northern fur seal research had difficulty in

finding evidence for a front passing through coastal Washington and British Columbia during March-May 1959-66. In surveys during 1959, the migratory front was assumed to have passed in late April during poor weather (Pike et al. 1959); in 1960 an increase in the number of females age >5 yr was found in Washington during April, but not in British Columbia during April-May (Pike et al. 1960); in 1961 the peak migration was thought to have been during the first half of April during poor observation conditions (Pike et al. 1961); in 1962 the peak migration was suspected to have been after sampling ended in late April (Pike et al. 1962); in 1963, the peak was thought to have been seen in the first half of May, but evidence was weak (Pike et al. 1963); and in 1966, the main migration was thought to have taken place prior to sampling in May (Pike and MacAskie 1966).

Second, sighting data from Manzer, Pike and MacAskie indicate that an increase in density of seals took place offshore in Region 1 during March-July (Fig. 9). The increase beginning in March coincided with the departure of seals from California in March. Thus, seals from California presumably moved into Region 1 in March-April. However, movement of these seals northward from Region 1 to offshore Regions 2-4 (Fig. 9) was not clearly evident. Perhaps, seals dispersed widely after leaving Region 1. The third source of evidence for an offshore migration from California to the Gulf of Alaska comes from an analysis of monthly and regional variations in pregnancy rates of females age 5+ yr. These data, which will be presented later (Pregnant females age 5+ yr), show that an expected increase in pregnancy rate from northward moving pregnant females from California does not materialize in Washington and British Columbia, but does in the Gulf of Alaska.

Evidence for an offshore migration of seals from Washington and British Columbia directly across the eastern North Pacific to the Eastern Aleutian Islands come from five sources. First, Ognev (1935) suggested that some offshore migration take places during February-March and May from Washington and the Eastern Gulf of Alaska. Second, Pike et al. (1960) and the Marine Mammal Biological Laboratory (1971) reported that seals in Washington appear to move offshore during April-June. Third, Manzer et al. (1969) concluded that most seals returning from coastal areas between southeast Alaska and California migrated offshore directly to the Eastern Aleutian Islands and the Pribilof Islands, although some were thought to take the coastal route. Fourth, Kajimura (1980, his Fig. 20-23) plotted the few offshore sightings collected during 1958-74 in the eastern North Pacific, plus the many sightings collected by other National Marine Fisheries Service research programs (Platforms of Opportunity Program, Outer Continental Shelf Environmental Assessment Program and Dall's porpoise program). His plots show that seals were particularly abundant in Regions 2 and 4 (Fig. 9) during June. This increase offshore coincided with the main

departure time of May-June for seals in Washington and British Columbia (Fig. 8). Finally, the relatively high density of seals in Region 1 during May-July (Fig. 9) could have resulted partially from the departure of seals from Washington in May-June. Similarly, the slight increase in density in Region 2 during June might result from the offshore migration from British Columbia. Presumably the late-leaving seals from Oregon and California in May-June would also take a direct offshore route to the Pribilof Islands. C. Fiscus (pers. comm., 21 April 1990) similarly suspects that some seals which leave late from California migrate directly across the eastern North Pacific.

I now summarize the proposed route and timing of migration for females age 3+ yr (Fig. 10a-b). These seals leave the Pribilof Islands during October-November, migrate south through Unimak Pass and directly across the eastern North Pacific to the coastal regions mainly between British Columbia and California with the vast majority travelling to California. No evidence exists that seals follow a coastline route from the Eastern Aleutian Islands to California. Manzer et al. (1969) also concluded that this is the route taken. Seals reach California in January and more northerly regions in December. The return migration begins during March in California when about half of the seals leave. Others in California do not leave until at least June. The California seals appear to use three return routes to the Pribilof Islands rather than one as previously believed. The main route is offshore to the Eastern and Western Gulf of Alaska which seals reach by April-May. Seals then migrate along the coast to the Eastern Aleutian Islands and to the Pribilof Islands by July-September. The second route from California courses northward along the coast to join the first route in the Eastern Gulf of Alaska. This was previously thought to be the main route. Some seals from Oregon, Washington and British Columbia may join the coastal migrating seals from California. The third return route is offshore from California and directly across the eastern North Pacific to the Eastern Aleutian Islands and the Pribilof Islands. Most seals in Washington and British Columbia, and perhaps Oregon, also appear to migrate offshore and directly to the Eastern Aleutian Islands, beginning their return migration in May-June.

FEMALES AGE 3-4 YR

The migration route of 3-4-yr-old nonpregnant females is assumed to be similar to that described for older females (Fig. 10a-b). As with older females, substantial numbers enter the coastal waters of the eastern North Pacific and also return to the Pribilof Islands. Females age 3-4 yr migrated mainly to Washington by December and California by January (Fig. 11). Their

density was about the same in California and Washington, which suggests that these ages were evenly distributed along the coast. However, most still migrated to California because California was the largest region. Very few females age 3-4 yr were likely to have migrated to Oregon, British Columbia and northward. This age group may not have begun to move into British Columbia from offshore until April-May. The density in California and Washington remained relatively stable from January-February to June, which suggests that females age 3-4 yr did not begin their return migration until after June.

Very few females age 3 yr moved into the Eastern Gulf of Alaska by June, but some influx of females age 4 yr was evident at this time. Thus, females age 4 yr arrived before age 3 yr. Large numbers of both ages moved into the Western Gulf of Alaska during July with 4-yr-olds tending to arrive earlier. More females age 4 yr reached the Pribilof Islands by August than 3-yr-olds. Females age 3 yr arrived in the Pribilof Island region mainly in September. However, Bigg (1986) suggested that the main arrival time for nonpregnant females age 3+ yr at haulouts on the Pribilof Islands was mid-August and thus earlier than indicated by the sighting data. The discrepancy probably results from the relatively small sample size of land data during August-September on which the arrival times of females age 3-4 yr were established. Thus, the arrival time given on land may be in error.

PREGNANT FEMALES AGE 5+ YR

Pregnant females (age 5+ yr) comprised the largest proportion of seals (52.5%, from Table 1) collected in coastal regions. An examination of the monthly variation in density of pregnant females within regions of the eastern North Pacific indicates that most migrated to California (Fig. 10a-b, 12). Pregnant females arrived mainly in January and reached a peak in numbers during February. Unlike the evenly distributed females of age 3-4 yr, the density in Washington was only about a third of that seen in California at this time. Because the density of all seals combined in Washington was about half that in California, pregnant females were disproportionately more abundant in California. Although the densities of pregnant females were not determined in Oregon, British Columbia and in more northern regions during January-February, their densities were likely to be low because the density for all population components combined was low in these regions (Fig. 8).

Unlike the late-leaving females of age 3-4 yr, pregnant females began their return migration from California in March, with others continuing to leave until June by which time very few

were left. Most pregnant females did not appear to move northward along the coast through Washington and British Columbia. No clear evidence exists of an increase in their density in these regions during March-April. The density remained relatively stable in Washington during December-April and in British Columbia during March-May. The first evidence of increased density of pregnant females after March was seen in the Eastern and Western Gulf of Alaska during April-May. Thus, the movement of pregnant females provides evidence for an offshore migration between California and the Gulf of Alaska.

Most pregnant females reached Western Alaska in June (Fig. 12; see also Fig. 8) and the Pribilof Islands in July. Only a few pregnant females remained in the Western Gulf of Alaska by July. A few were still present off California in June and most did not depart from Washington and British Columbia until May-June. Because of the short period of time between departure in the coastal regions of the eastern North Pacific and the arrival time on the Pribilof Islands to pup (July), some pregnant females from regions in California and most in Washington and British Columbia probably travelled directly across the eastern North Pacific to the Pribilof Islands.

The density of pregnant females in the Pribilof Islands region remained stationary from July until at least September. A stationary density was expected because pregnant females give birth on the Pribilof Islands mainly in July and remain in the region to nurse their pups until October-November (Peterson 1968; Gentry and Holt 1986). Some pregnant (postpartum) females travelled from the Pribilof Islands to Unimak Pass during August-September (Table 2).

NONPREGNANT FEMALES AGE 5+ YR

The migratory route of nonpregnant females age 5 yr is assumed to be similar to that of other females age 3+ yr (Fig. 10a-b). However, nonpregnant females tended to return after pregnant females. As with pregnant females of this age, the main arrival time in Washington was December and in California was January. Similarly, most nonpregnant females travelled to California (Fig. 13) with the peak density in California during February. Although the density in California was not much greater than in Washington, when regional sizes were taken into consideration, relatively few migrated to Washington and British Columbia or to the north.

Differences between the timing of the return migration by nonpregnant and pregnant females age 5+ yr were determined from an examination of pregnancy rates by month and region. If

nonpregnant and pregnant females migrated along the same route and at the same time, the observed and expected pregnancy rates by month and region would be the same. The expected pregnancy rate for an equilibrium population was 76.4% (from Table 1). However, the observed pregnancy rate by month and region was quite variable (Table 3). The rate was higher than expected in California when pregnant females first arrived during January-February, but near or lower than expected in more northern regions at this time. These data suggest that a slight tendency might exist for nonpregnant females age 5+ yr not to travel as far south as pregnant females by January-February.

Also, a gradual decline in pregnancy rate took place in California between March and June. The decline suggests that nonpregnant females tended to return to the Pribilofs after pregnant females. The earlier departure of pregnant females suggests that if they migrated from California northward along the coastal route to the Gulf of Alaska, then an increased pregnancy rate should have been evident in Oregon, Washington and British Columbia during March-May. However, such an increase was not observed. The pregnancy rate in Oregon, Washington and British Columbia remained at the expected or lower level during December-May. The first evidence of females with a high pregnancy rate was seen in the Eastern and Western Gulf of Alaska during April. Thus, the pregnancy rate data provide evidence which is independent from sighting data that an offshore route exists for returning seals that travel from California to the Gulf of Alaska.

The pregnancy rates indicate further that the migratory front of pregnant females passed through Western Alaska (Fig. 13; see also Fig. 8) and Eastern Aleutian Islands (Table 2) in June and reached the Pribilof Islands in July. Lowered pregnancy rates were evident after the front passed through the Eastern and Western Gulf of Alaska and the Eastern Aleutian Islands. Thus, in regions north of California nonpregnant females age 5+ yr continued to migrate after pregnant females. Taylor et al. (1955) similarly reported that nonpregnant females on their return migration arrived in the Western Gulf of Alaska after pregnant females.

Nonpregnant females age 5+ yr continued to increase in density in the Pribilof Islands region during August. This suggests that some did not reach the Pribilof Islands until up to about a month after pregnant females. Their arrival resulted in a decline in pregnancy rate (Table 3). The later arrival of nonpregnant females supports the analysis of kill data from the Pribilof Islands (Bigg 1986) that indicate some nonpregnant females age 4+ yr do not arrive at the Pribilof Islands until August, or about one month later than pregnant females of the same age.

A particularly high pregnancy rate existed in the Pribilof Islands region during July-September (Table 3). This high rate probably resulted from nonpregnant females age 5+ yr tending to reside to the south in the Eastern Aleutian Islands, as indicated by the low pregnancy rate there. Another possible reason for the high rate in the Pribilof Islands region might be that nonpregnant females tended to haul out on the Pribilof Islands for longer periods of time than pregnant females. However, this seems unlikely to be the case because behavioral observations suggest that nonpregnant adult females are on land for only 10% of their time whereas females with nursing pups are on land 27% of the time (Gentry and Holt 1986; French et al. 1989).

DISCUSSION

HABITAT AND FOOD

Dingle (1985) points out that migration is an important component of an animal's life history strategy. Migration allows an animal to escape from a seasonally unfavorable habitat and to exploit one which is more favorable. By migrating an individual can increase its fitness through improved reproduction and survival. The migration of northern fur seals that breed on the Pribilof Islands appears to reflect these principles. During June-October, most of this stock moves from the eastern North Pacific to the Pribilof Islands and surrounding waters. However, the Pribilof Islands does not appear to be a suitable habitat for northern fur seals at other times of the year. This seal appears to avoid a cold environment. Seasonal ice covers much of the Bering Sea during winter-spring with drift ice extending south of the Pribilof Islands during February-April (Brower et al. 1977). The seal rarely hauls out on ice and does not use ice breathing holes as do arctic dwelling pinnipeds. Also, cold stormy weather with snow begins abruptly during November (Jordan and Clark 1898). Thus, the departure of most seals from the Pribilof Islands in October-November coincides with the onset of a cold environment. At this time the seal seeks space and food in the eastern North Pacific for the winter and spring period. Its return to the Pribilof Islands in June coincides with the retreat of ice from this region and the onset of warmer weather.

Another important factor that governs the migration of animals is the availability of food (Baker 1978; Dingle 1985). The possible role that food has played in the development of migration for the Pribilof Islands stock can be inferred from an

examination of the seasonal changes in abundance of the seal and the seasonal changes in diet along its migratory route. Kajimura (1985) and Perez and Bigg (1986) described the monthly and regional variation in diet of this stock. They analyzed the stomach contents of individuals from the same data base collected during 1958-74 as used in the current study. Although neither study considered diet by sex and age, the largest component (52.5%) in the diet studies and in the current study was pregnant females age 5+ yr.

At the time of peak abundance of seals in California, during January-February, their diet was dominated by northern anchovy (Engraulis mordax), which comprised about 50% of the food consumed (Perez and Bigg 1986). Pacific whiting (Merluccius productus), Pacific saury (Cololabis saira) and squid were also eaten at this time. The departure of about half the seals in March coincided with a sharp drop in consumption of northern anchovy. By March northern anchovy decreased to 25% of the diet and by April to only 10%. Seals that remained in California until June fed upon mainly Pacific whiting plus northern anchovy, Pacific saury and market squid (Loligo opalescans). The seals that inhabited Oregon, Washington and British Columbia between December and May-June fed on a wide variety of prey species. The prey species included mainly northern anchovy, Pacific whiting, rockfishes (Sebastes spp.), Pacific herring (Clupea harengus pallasi), salmonids (Salmonidae), market squid and onychoteuthid squids. Northern anchovy were particularly important in Oregon and Washington and Pacific herring were particularly important in Washington and British Columbia. During February-March the diet of seals in the Eastern Gulf of Alaska was known only for Sitka Sound where essentially only Pacific herring were eaten.

When returning seals from California reached the Gulf of Alaska they fed mainly upon capelin (Mallotus villosus) and Pacific sand lance (Ammodytes hexapterus). During April-June these two species together constituted about 74% (32% capelin; 42% Pacific sandlance) of the diet. Walleye pollock (Theragra chalcogramma), salmonids and gonatid squid were also eaten. As seals moved west along the coast to Western Alaska and the Eastern Aleutian Islands in June-July they continued to feed mainly upon Pacific sand lance and capelin, but also consumed Atka mackerel (Pleurogrammus monopterygius), Pacific herring, sablefish (Anoplopoma fimbria) and squid (Berryteuthis magister).

When seals entered the Pribilof Islands region in July their diet changed to mainly walleye pollock. During July-September, walleye pollock comprised about 55% of the diet around the Pribilof Islands (Perez and Bigg 1986). Also, Kajimura (1985) reported that walleye pollock comprised 82-86% of the prey volumes of seals collected near the Pribilof Islands in 1973-74. Seals which remained in the Eastern Aleutian Islands region during July-September fed principally on capelin.

The diet of seals that remained offshore or travelled through offshore regions probably consists mainly of squid. An examination of stomachs of seals collected off the continental shelf in the eastern North Pacific indicated that gonatid and onychoteuthid squid were the most important prey, with some salmonids and rockfishes also eaten (Perez and Bigg 1986). Similarly, seals taken off the continental shelf in the eastern Bering Sea had mainly gonatid squids in their stomachs.

These diet studies and those undertaken on Asian stocks indicate that northern fur seals prefer to feed upon small schooling fish (Perez and Bigg 1986). An examination of the localities where large biomasses of small schooling fishes exist suggests the role that prey biomass has played in migration. The largest fish biomass along the seals' migratory route is walleye pollock in the eastern Bering Sea. Walleye pollock is the dominant fish species in the eastern Bering Sea with a mean biomass of 8.4 mill. mt during 1964-86 (Bakkala 1989). Although walleye pollock is a schooling fish with large adults, northern fur seals feed mainly upon the juveniles (Perez and Bigg 1986). Presumably, it is the huge biomass of walleye pollock in the eastern Bering Sea that has allowed the stock to establish its large rookeries there. It should be noted at this point that walleye pollock biomass has increased considerably over the past 25 years. However, this species could still have played an important role in the evolution of migration of northern fur seals. Other prey species (e.g. Pacific sardine, northern anchovy) in the eastern North Pacific will be shown to have also varied considerably in biomass over many years.

The potential feeding areas in the eastern North Pacific for seals can be divided into two main coastal fish producing domains, the Coastal Downwelling Domain and the Coastal Upwelling Domain (Ware and McFarlane 1989). The Coastal Downwelling Domain extends from about central British Columbia north and west along the coast to the Aleutian Islands. The fish species which are consumed by seals in this domain consist mainly of walleye pollock (biomass 1.50 mill. mt), which is restricted to the Western Gulf of Alaska and west to the Aleutian Islands, and of Pacific herring in northern British Columbia (.21 mill. mt). No estimates are available for the biomass of Pacific sand lance and capelin which are the commonly eaten prey species by seals in the Gulf of Alaska during April-July. These fish species are apparently not abundant enough to support a commercial fishery of any significance although they probably still comprise quite a large biomass (J. Blackburn, Alaska Dep. Fish and Game, Kodiak, pers. comm. February, 1990).

The Coastal Upwelling Domain extends from central British Columbia south to 32°N in Baja California. The production of fish consumed by seals within the seal's range in this domain include mainly northern anchovy (1.37 mill. mt), Pacific hake

(1.50 mill. mt), Jack mackerel (.97 mill. mt) and Pacific herring (.13 mill. mt). The abundance of some prey species within this domain has changed over the years and thus the relative importance of each prey species to northern fur seals has also probably varied. For example, although the Pacific sardine (Sardinops sagax) was not recorded as a prey species during 1958-74, it may have been an important food before depletion by commercial fishing prior to 1950 (Perez and Bigg 1986). The biomass of Pacific sardine is currently small (<.02 mill. mt), but before 1950 was large (1.2 mill. mt). Also, the abundance of the Pacific sardine has fluctuated considerably over the past 1850 years (Soutar and Isaacs 1969). In addition, the biomass of northern anchovy was estimated to be 3-4 times larger 1100 years ago than it has been in recent years.

These data indicate that during winter, the Pribilof Islands stock migrates primarily to the Coastal Upwelling Domain where a large biomass of small schooling fishes exists. This conclusion is also supported by the hunting patterns of pelagic sealers in the late 1800's. They reported that, during winter and early spring, seals were most abundant in the eastern North Pacific in the regions within this domain. During winter and early spring, the sealers hunted in two sealing grounds, the Farallon Grounds and the Vancouver Grounds (Townsend 1899). The Farallon Grounds were located along the coast of California from about 36°N to Cape Mendicino and the Vancouver Grounds were located from Yaquina Bay (Oregon) to northern Vancouver Island. Presumably, the Coastal Downwelling Domain is not as suitable to seals because the available biomass of small schooling fish is less than the Coastal Upwelling Domain. Although a large biomass of walleye pollock exists in the western portion of this domain, this fish is not important in the diet of seals that migrate through the western portion in April-July. The reason that this fish is not eaten may be that, although juvenile pollock are available in the coastal waters of the Gulf of Alaska, they do not form dense concentrations there (E. Nunnelle, Alaska Fish. Sci. Center, Seattle, pers. comm, February 1990) and thus might not be particularly available to seals. On the other hand, Pacific sand lance and capelin do form dense concentrations and seals could feed preferentially upon them.

INHERENT AND LEARNED MIGRATION

Baker (1978) notes that migration in animals is determined by an interaction between inherent and learned migratory behaviors. Inherent migratory behaviors result from evolution and include the control of migratory season, direction and distance. These behaviors are triggered by physiological responses to such factors as photoperiod, temperature and

endogenous rhythms. Learned migratory behaviors can change with experience and include learning the location of food, competition and predation. Inherent behaviors provide the tendencies for an animal to undertake a migration and learned behaviors modify the tendencies to improve survival.

The question now arises as to what extent inherent and learned behaviors control the migration of northern fur seals between the eastern Bering Sea and the Coastal Upwelling Domain. In the following discussion I will focus on some of the ideas developed by Baker (1978) regarding the control of migration in northern fur seals. Baker stated that sexual maturation controls the initiation of migration in many vertebrates and suggests that this is probably also true for northern fur seals. Thus, the migratory drive would begin at maturation. Bigg (1986) examined this possibility and reported that the process of gradual maturation within a cohort of northern fur seals was correlated with a progressively increasing proportion of individuals that return to the Pribilof Islands. Very few individuals age 1 yr returned, a greater proportion returned at age 2 yr and most did so by maturation at 3-5 yr of age.

Bigg (1986) also reported that gradual maturation of a cohort was correlated with progressively earlier arrival times on the Pribilof Islands by each sex. For example, bulls arrived first in May-June to establish territories on rookeries (see also Peterson 1968). Younger males (<5 yr) returned progressively later (up to October) with decreasing age and hauled out adjacent to rookeries. Pregnant females arrived on rookeries by mid-July to give birth and then nursed their pups until October-November. Immature females returned to hauling grounds beginning in August and progressively later (up to November) with decreasing age.

The current study similarly shows that the return migration for each population component in the eastern North Pacific parallels that for their arrival schedule at the Pribilof Islands. Also, more individuals undertake the return migration and the migration takes place earlier with approaching maturity. Thus, sexual maturation appears to initiate migration and alter the season of migration.

Regarding direction and distance in migration of northern fur seals, Baker felt no inherent tendency may exist. Instead he felt that these features were learned. He suggested that pups first explored around the Pribilof Islands and eventually located the eastern North Pacific to the south. Once in the eastern North Pacific pups began a broad exploration to establish a familiar area and over the next few years the seals learned to migrate to preferred areas that differ for each sex and age.

However, an inherent tendency for a migratory direction could exist. For example, pups typically leave the Pribilof Islands in November and enter the eastern North Pacific shortly after in December. They seem unlikely to explore randomly in the eastern Bering Sea because pups have never been seen in waters north of the Pribilof Islands during November-December (Marine Mammal Biological Laboratory 1970). Further, some pups do not find the passes in the Eastern Aleutian Islands and have been observed moving southward overland on the Alaska Peninsula in fall and winter. Once in the eastern North Pacific some pups migrate rapidly south and east because they arrive on the coast between the Western Gulf of Alaska and California by December (Kajimura 1980). Pups do not follow their mothers to the coast because they separate at weaning on the Pribilof Islands (Gentry and Holt, 1986) and seals tend to migrate individually.

An inherent tendency for females to migrate greater distances than males could also exist. With increasing age, males tend to remain in Alaska whereas females tend to travel to California. Jordan and Clark (1898) reported that some young males (presumably about age 3-5 yr) and bulls stay near the Pribilof Islands after most seals have left and in mild winters stay there all winter. Females do not do this and instead tend to travel to California. The tendency for the two sexes to migrate different distances begins at about age 3 yr, which coincides with the onset of sexual maturity. Thus, the onset of sexual maturation might initiate a tendency for differential migratory distance by each sex as well as other aspects of migration.

The current study indicates that as females mature they increase in number along the coast of the eastern North Pacific during winter. Except for yearlings in Washington and British Columbia, this is the case for females between ages 1 and 5+ yr. Baker's view would be that the increased numbers along the coast reflects the seals' discovery of good foraging habitat. However, these data could be interpreted just as well to support an inherent tendency to migrate to particular latitudes and longitudes which is expressed more strongly as a cohort matures.

The movement of yearling males and females into Washington and British Columbia during February-April is probably not a migration, but rather a passive drift into these regions from offshore. Yearlings are presumably carried into these regions by the Subarctic Current, which travels from the Asian coast to the North America coast where it splits north and south off Washington and British Columbia (Thomson 1981). If the yearling movement into Washington and British Columbia was a migration then seals would be expected to return in similar numbers at age 2 yr, but they do not. By their second year, seals have probably found a feeding area offshore and actively remain there rather than drifting into shore. Alternatively, yearlings might migrate to these coastal waters, where they learn to become

proficient foragers, and then can remain offshore in their second year.

While evidence for directionality and distance in migration is only circumstantial, selection for such inherent characteristics would seem to provide survival advantages for the long migration between the Pribilof Islands and the coast of the eastern North Pacific. When seals leave the Pribilof Islands most do not approach land again until they return. Directionality would make the departure from the Pribilof Islands more efficient by preventing seals from travelling north into the advancing ice and would increase the chances of locating coastal food supplies in the eastern North Pacific and of successfully returning to the Pribilof Islands. A mechanism to control distance of migration in each sex might reduce food competition between the sexes.

The evolution of the physiological mechanisms that control the route and timing of migration would likely involve many selective factors. For example, the departure time from the Pribilof Islands would likely be affected by the seasonal timing of cold weather and the advancing ice pack as well as the duration of lactation. The departure time from the wintering regions would likely be influenced by the time required to return to the rookeries. Also, the sequence of the return migration by sex, age and reproductive condition is likely to be influenced by competition for food and space, energetic requirements and the various reproductive needs of each sex and age.

Some examples of learned behaviors now follow. Seals seem to learn the location of some local food sources and return to them each year. Seals enter the inlets of Sitka Sound and the inshore waters of northern Hecate Strait to feed on Pacific herring during January-March (Kenyon and Wilke 1953; Taylor et al. 1955; Kajimura 1985; Perez and Bigg 1986). Also, the location where seals aggregate can change each year depending upon the movement of prey species. For example, the main feeding area at Unimak Pass during July-October 1962 was to the north and northwest of the pass (Fiscus el al 1964). In 1963, the location shifted to about 90 km west (Fiscus, et al. 1965) and in 1964 relatively few seals were seen north of the pass (Fiscus and Kajimura 1965). Kajimura (1985) examined the likely availability of prey species over the stocks' coastal distribution and concluded that this is an opportunistic feeder that searches out local concentrations of food.

The seals found along the coast between British Columbia and California consist primarily of females. If an inherent tendency existed for females to migrate eastward from offshore toward these regions, learning could still play an important role in determining the specific distribution of these seals along the coast. Although females age 1-4 yr are relatively evenly distributed along the coast, by age 5+ yr they aggregate

in California. Thus, the best foraging locations along the coast could be learned by older seals and these seals would tend to migrate there.

A combination of learned and inherent behaviors might explain the unusual timing and unexpected offshore return route from California to the Gulf of Alaska for pregnant females. Pregnant females in California begin their return migration during March at which time about half leave and travel offshore to the Gulf of Alaska with others leaving as late as June. On the other hand, most females in Washington and British Columbia leave in May-June and appear to travel directly offshore to the Eastern Aleutian Islands. Females in the Gulf of Alaska depart during June-July and travel west along the coast. I propose the following explanation for this migratory pattern. Pregnant females leave California in March because they have learned that the availability of their main food supply decreases at this time and that a more suitable supply exists in the Gulf of Alaska. Support for this contention comes from the strong correlation between the departure of pregnant females from California in March and the declining consumption of their main food, northern anchovy, during March-April. However, the food supply for the seals in Washington and British Columbia presumably does not decrease which allows females to remain there until May-June. An offshore route from California to the Gulf of Alaska may be taken because it is the most direct path by which to get there. Alternatively, a more abundant food supply for migrating seals could exist offshore. Such a food supply could have been learned from the earlier years spent offshore.

This learned migration could result from two feeding strategies of adult females. Females in California might specialize in foraging on a relatively few but abundant prey species, such as northern anchovy in California and Pacific sand lance and capelin in the Gulf of Alaska. Females in Washington and British Columbia might specialize in foraging on numerous prey species, none of which is particularly abundant or available, but together can support a local population of northern fur seals from December to June. Similar differences in feeding strategies exist in the humpback whale (Megaptera novaeangliae) in the Western Atlantic Ocean (Katona and Baird 1990). Individually recognizable whales are known to migrate from calving and breeding areas during winter in the West Indies north to 5-6 separate summer feeding grounds located between the Gulf of Maine and Iceland.

A physiological stimulus is presumably involved at some point in the initiation of the return migration of pregnant females between California and British Columbia. Perhaps this stimulation takes place mainly in May-June when pregnant females are distributed widely along the coast from California to the Gulf of Alaska. At this time, all females appear to begin their

return migration to the Pribilof Islands in a broad front to reach the Pribilof Islands in July. Thus, some early movements by pregnant females, such as those females leaving California in March, could be due to learning, but then a common physiological stimulus for migration might be expressed in May-June.

An interesting natural experiment is taking place at the two newly established colonies off western North America at San Miguel Island and Bogoslof Island. Studies at these new colonies may eventually provide insights into the roles of learned and inherent behaviors in migration of the Pribilof Islands stock. Based on tagged individuals, the original colonizers at San Miguel Island came from the Robben Island, Commander Islands and Pribilof Islands stocks (North Pacific Fur Seal Commission 1975) and those at Bogoslof Island came from the Commander Islands and presumably the Pribilof Islands (Loughlin and Miller 1989). These new colonies have grown from both reproduction and new colonizers. The fact that colonizers remain at the new rookeries suggests that learning can, at least temporarily, override any inherent tendency for seals to return to their natal rookeries.

Baker (1978) predicted that if a directional migratory tendency existed then the colonizers at San Miguel should tend to travel south after breeding, unless the warmer waters to the south stopped them from doing so. Also, if the tendency for males to utilize the Gulf of Alaska rather than more southern regions is learned, as he feels it is, then adult males of the San Miguel Island stock will learn to travel there. However, not enough data have been collected yet to examine these predictions.

DeLong and Antonelis (in press) have undertaken flipper tagging of seals at San Miguel Island and eventually may have enough data to test Baker's predictions. Based on the recovery of 46 tagged individuals, most young seals (pups-4 yr) from San Miguel Island remain off California although some reach Oregon and British Columbia. These observations are equivocal for understanding migratory control in that the seals may have learned of good feeding areas locally and to the north or they may have been directed to particular latitudes by an inherent mechanism. However, an important observation was made of a male which was tagged as a pup on San Miguel Island and three years later was sighted on the Pribilof Islands (Antonelis and DeLong 1986). This observation would seem to support more strongly the existence of an inherent component to locate the Pribilof Islands rather than a chance finding of this site by the seal.

However, at this point assessments of the relative importance of learned and inherent behaviors associated with migration can be only speculative. Experimental studies are needed to observe the migratory patterns of seals under different situations. Satellite tracking of the seasonal movements of seals

of various ages offers particular hope in this regard. Such studies could determine the development of migration from the Pribilof Islands and that of new colonizers. Also, such studies might determine whether location imprinting of neonates plays a role in migration. Imprinting is important in the development of behavior in many animals (Hess 1973), but has not yet been considered in migration studies of northern fur seals.

ACKNOWLEDGEMENTS

I wish to thank I. Fawcett, M. Hladyschevsky and K. Hobbs for their tireless and careful efforts in preparing summaries of population composition data from computer printouts and M. Marshall for writing the numerous computer programs needed to examine the northern fur seal data base. I am also very grateful for the generosity of J. Manzer (retired), G. Pike (deceased) and I. B. MacAskie (retired) for allowing me to use their unpublished data on the relative abundance of northern fur seals in coastal and offshore regions. The following people made valuable comments on the manuscript: R. DeLong, G. Ellis, C. Fiscus, A. Trites and two anonymous reviewers.

LITERATURE CITED

Antonelis, G. A., and R. L. Delong. 1986. Population and behavioral studies, San Miguel Island, California. In P. Kozloff (editor), Fur seal investigations, 1984, p. 49-53. NOAA Tech. Mem. NMFS F/NWC-97.

Baker, R. R. 1978. The evolutionary ecology of animal migration. Holmes and Meier Publ. N.Y., 1012 p.

Bakkala, R. 1989. Variability in the size and age composition of eastern Bering Sea walleye pollock. In Proceedings of the international symposium on the biology and management of walleye pollock, p. 307-322; Anchorage, Alaska, 14-16 November 1988, Alaska Sea Grant Program, University of Alaska, Fairbanks, Alaska.

Bigg, M. A. 1982. Migration of northern fur seals in the eastern North Pacific and eastern Bering Sea: an analysis using effort and population composition data. Unpubl. MS.

49 p. Dep. Fish. Oceans, Pacific Biol. Stn., Nanaimo, British Columbia.

1986. Arrival of northern fur seals, Callorhinus ursinus, on St. Paul Islands, Alaska. Fish. Bull. 84:383-394.

Bissett. 1890'S. Captain Bissett's report. In F. A. Zeusler, 1936, Report of the oceanographic activities of the U.S. Coast Guard Cutter Chelin during the summer of 1934. Unpubl. mimeographed report, p. 38-40. Available at United States Department of Commerce, NOAA, National Marine Fisheries Service, National Marine Mammal Laboratory, 7600 Sand Point Way NE, Seattle, Washington 98115, U.S.A.

Brower, W. A., H. F. Diaz, A. S. Prechtel, H. W. Searby, and J. L. Wise. 1977. Climate atlas of the outer continental shelf waters and coastal regions of Alaska. Vol.2, Bering Sea. U.S. Dep. Commer., National Oceanic and Atmospheric Administration, Alaska Outer Continental Shelf Environmental Assessment Program, Final Report - Research Unit No. 347.

Craig, A. M. 1964. Histology of reproduction and the estrus cycle in the female fur seal, Callorhinus ursinus. J. Fish. Res. Bd. Canada 21:773-811.

Delong, R. L. 1982. Population biology of northern fur seals at San Miguel Island, California. PhD thesis, University of California, Berkeley.

Delong, R. L., and G. A. Antonelis. In press. Impact of the 1982-1983 El Niño on the northern fur seal population at San Miguel Island, California. In F. Trilmich, and K. Ono (editors), Pinnipeds and El Niño: responses to environmental stress. Univ. Calif. Press, Berkeley.

Dingle, H. 1985. Migration and life histories. In M. A. Rankin, D. Checkley, J. Cullen, C. Kitting, and P. Thomas (editors), Migration: mechanisms and adaptive significance, p. 27-42. Contributions in Marine Science, Supplement Vol. 27.

Fiscus, C. H. 1986. Northern fur seal. In D. Haley (editor), Marine mammals of eastern North Pacific and arctic waters, p. 174-181. Pac. Search Press, Seattle, WA.

Fiscus, C. H., K. Niggol, and F. Wilke. 1961. Pelagic fur seal investigations, California to British Columbia, 1961. U.S. Fish Wildl. Serv., Seattle, Washington. Processed Rept. 87 p.

French, D. P., M. Reed, J. Calambokidis, and J.C. Cubbage. A simulation model of seasonal migration and daily movements of the northern fur seal. Ecol. Modelling 48:193-219.

Gentry, R. L., and J. R. Holt. 1986. Attendance behavior of northern fur seals. In R. L. Gentry, and G. L. Kooyman (editors), Fur seals: maternal strategies on land and at sea, p. 41-60. Princeton Univ. Press, New Jersey.

Hess, E. H. 1973. Imprinting; early experience and the developmental psychobiology of attachment. Van Nostrand Reinhold Co., N. Y., New York.

Hooper. 1892. Report of Captain Hooper, U.S.R.M., 21 November, 1892. In F. A. Zeusler, 1936, Report of the oceanographic activities of the U.S. Coast Guard Cutter Chelin during the summer of 1934. Unpubl. mimeographed report, p. 40-44. Available at United States Department of Commerce, NOAA, National Marine Fisheries Service, National Marine Mammal Laboratory, 7600 Sand Point Way NE, Seattle, Washington 98115, U.S.A.

Jordan, D. S., and G. A. Clark. 1898. The history, condition, and needs of the herd of fur seals resorting to the Pribilof Islands. In D. S. Jordan, L. Stejneger, F. A. Lucas, J. F. Moser, C. H. Townsend, G. A. Clark, and J. Murray (editors), The fur seals and fur-seal islands of the North Pacific Ocean, Part 1, 249 p. Treas. Dep. Doc. 2017, 4 parts.

Kajimura, H. 1979. Fur seal pup/yearling distribution in the eastern North Pacific. In H. Kajimura, R. H. Lander, M. A. Perez, A. E. York, and M. A. Bigg (editors), Preliminary analysis of pelagic fur seal data collected by the United States and Canada during 1958-74, p. 9-49. Unpubl. MS. National Marine Mammal Laboratory, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA

1980. Distribution and migration of northern fur seals (Callorhinus ursinus) in the eastern Pacific. In H. Kajimura, R. H. Lander, M. A. Perez, A. E. York, and M. A. Bigg (editors), Further analysis of pelagic fur seal data collected by the United States and Canada during 1958-74, p. 6-43. Unpubl. MS. National Marine Mammal Laboratory, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA.

1985. Opportunistic feeding by the northern fur seal, (Callorhinus ursinus). In J. R. Beddington, R. H. J. Beverton, and D. M. Lavigne (editors), Marine mammals and fisheries, p. 300-318. George Allen and Unwin (Publ.), Lond.

Katona, S. K., and J. A. Baird. (in press). Population size, migration and feeding aggregations of the humpback whale (Megaptera novaeangliae) in the Western Atlantic Ocean. Rep. int. Whal. Commn (Special issue 12).

Kenyon, K. W., and F. Wilke. 1953. Migration of the northern fur seal, Callorhinus ursinus. J. Mammal. 34:86-98.

King, J. E. 1983. Seals of the world. British Museum (Natural History), Oxford Univ. Press, Oxford, 240 p.

Lander, R. H. 1980. A life table and biomass estimate for Alaskan fur seals. In H. Kajimura, R. H. Lander, M. A. Perez, A. E. York, and M. A. Bigg (editors), Further analysis of pelagic fur seal data collected by the United States and Canada during 1958-74, p. 44-57. Unpubl. MS. National Marine Mammal Laboratory, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA.

1980 (editor). Summary of northern fur seal data and collection procedures. Vol. 2: Eastern Pacific pelagic data of the United States and Canada (excluding fur seals sighted). U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-4, 541 p.

1981. A life table and biomass estimate for the Alaska fur seals. Fish. Res. 1:55-70.

Loughlin, T. R., and R. V. Miller. 1989. Growth of the northern fur seal colony on Bogoslof Island, Alaska. Arctic 42:368-372.

Manzer, J. I., G. C. Pike, and I. B. Macaskie. 1969. Distribution and migration of northern fur seals in the northeast Pacific Ocean. Unpubl. MS. 41 p. Dep. Fish. Oceans, Pacific Biol. Stn., Nanaimo, British Columbia.

Marine Mammal Biological Laboratory. 1970. Fur seal investigation, 1967. U.S. Fish Wildl. Serv., Spec. Sci. Rept. 597.

1971. Fur seal investigations, 1970. National Marine Fisheries Service, National Marine Mammal Laboratory, 7600 Sand Point Way NE, Seattle, Washington 98115, U.S.A.

Loughlin, T. R., and R. V. Miller. 1989. Growth of the northern fur seal colony on Bogoslof Island, Alaska. Arctic 42:368-372.

Niggol, K., C. H. Fiscus, T. P. O'Brien, and F. Wilke. 1960. Pelagic fur seal investigations, Alaska, 1960. U.S. Fish and Wildl. Serv., Seattle, Washington. Processed Rept. 61 p.

North Pacific Fur Seal Commission. 1962. North Pacific Fur Seal Commission report on investigations during 1958-61. North Pac. Fur Seal Comm., Wash. DC, 183 p.

1969. North Pacific Fur Seal Commission report on investigations during 1964-66. North Pac. Fur Seal Comm., Wash. DC, 161 p.

1971. North Pacific Fur Seal Commission report on investigations during 1962-63. North Pac. Fur Seal Comm., Wash. DC, 96 p.

1975. North Pacific Fur Seal Commission report on investigations during 1967-72. North Pac. Fur Seal Comm., Wash. DC, 161 p.

1980. North Pacific Fur Seal Commission report on investigations during 1973-76. North Pac. Fur Seal Comm., Wash. DC, 197 p.

1984. Proceedings of the 27th Annual Meeting April 9-13, 1984, Moscow, U.S.S.R. North Pac. Fur Seal Comm., Wash., DC, 50 p.

Ognev, S. I. 1935. Mammals of U.S.S.R. and adjacent countries. Vol. 3. Carnivora (Fissipedia and Pinnipedia). Israel Prog. Scient. Transl., Jerusalem (1962), 656 p.

Perez, M. A., and M. A. Bigg. 1986. Diet of northern fur seals, Callorhinus ursinus, off western North America. Fish. Bull. 84:957-971.

Peterson, R. S. 1968. Social behaviour of pinnipeds, with particular reference to the northern fur seal. In R. J. Harrison, R. C. Hubbard, R. S. Peterson, C. E. Rice, and R. J. Schusterman (editors), The behavior and physiology of pinnipeds, p. 3-53. Appleton-Century-Crofts, N.Y., 411 p.

Peterson, R. S., B. J. Le Boeuf, and R. L. Delong. 1968. Fur seals from the Bering Sea breeding in California. Nature 219:899-901.

Pike, G. C., D. .J. Spalding, I. B. Macaskie, and A. Craig. 1959. Preliminary report on Canadian pelagic fur seal research in 1959. Fish. Res. Board Can. 51 p.

1960. Report on Canadian pelagic fur seal research in 1960. Fish. Res. Board Can. 92 p.

1961. Report on Canadian pelagic fur seal research in 1961. Fish. Res. Board Can. Man. Rep. Series (Biological) 719, 35 p.

1962. Report on Canadian pelagic fur seal research in 1962. Fish. Res. Board Can. Man. Rep. Series (Biological) 736, 35 p.

1963. Report on Canadian pelagic fur seal research in 1963. Fish. Res. Board Can. Man. Rep. Series (Biological) 761, 29 p.

Pike, G. C., and I. B. MacAskie. 1966. Report on Canadian pelagic fur seal research in 1966. Fish. Res. Board Can. MS Rep. Series (Biological) 875, 20 p.

Scheffer, V. B. 1958. Seals, sea lions and walruses. A review of the Pinnipedia. Stanford University Press. Lond. 179 p.

Soutar, A. and J. D. Isaacs. History of fish populations inferred from fish scales in anaerobic sediments off California. Calif. Coop. Oceanic Fish. Invest. Rep. 13:63-70.

Taylor, F. H. C., M. Fujinaga, and F. Wilke. 1955. Distribution and food habits of the fur seals of the North Pacific Ocean. U.S. Dep. Inter., Fish Wildl. Serv., Wash., DC, 86 p.

Thomson, R. E. 1981. Oceanography of the British Columbia coast. Can. Spec. Publ. Fish. Aquat. Sci. 56.

Townsend, C. H. 1899. Pelagic sealing. In D. S. Jordan, L. Stejneger, F. A. Lucas, J. F. Moser, C. H. Townsend, G. A. Clark, and J. Murray (editors), The fur seals and fur-seal islands of the North Pacific Ocean, p. 223-274, Part 3, 629 p. Treas. Dep. Doc. 2017, 4 parts.

Ware, D. M., and G. A. McFarlane. 1989. Fisheries production domains in the northeast Pacific Ocean. In R. J. Beamish and G. A. McFarlane (editors), Effect of ocean variability on recruitment and an evaluation of parameters used in stock assessment models, p. 359-379. Can. Spec. Publ. Fish. Aquat. Sci. 108.

Wilke, F., K. Niggol, and C. H. Fiscus. 1958. Pelagic fur seal investigations, California, Oregon, Washington, and Alaska, 1958. U.S. Fish Wildl. Serv., Seattle, Washington. Processed Rept. 96 p.

Zeusler, F. A. 1936. Report of the oceanographic activities of the U.S. Coast Guard Cutter Chelin during the summer of 1934. Unpubl. mimeographed report p. 50-67. Available at United States Department of Commerce, NOAA, National Marine Fisheries Service, National Marine Mammal Laboratory, 7600 Sand Point Way NE, Seattle, Washington 98115, U.S.A.

Table 1. Percent composition of each sex and age in an equilibrium population of northern fur seals age 1+ yr, based on Lander (1980[1], 1981) and in collections for all regions combined during 1958-74.

	Equilibrium Population			All regions		
	Female			Female		
Age	NP[2]	P[2]	Male	NP	P	Male
1	8.8	0.0	8.4	4.0	0.0	3.1
2	7.1	0.0	6.4	2.4	0.0	2.3
3	5.9	0.0	5.0	5.7	0.0	2.9
4	5.3	0.2	4+ 6.8	7.6	0.2	4+ 2.8
5+	10.9	35.2		16.4	52.5	
Total	38.0	35.4	26.6	36.1	52.7	11.1

[1]Lander (1980) was used for the natural mortality rate of females age 2 yr because a typographical error appears to exist for this rate in Lander (1981).

[2]NP = nonpregnant; P = pregnant

Table 2. Percent composition of each sex and age from collection of northern fur seals in the Eastern Aleutian Islands and Sitka Sound during 1958-74.

Topic	Eastern Aleutian Islands							Sitka Sd	
	May	Jun[2]	Jul	Aug[2]	Sep[2]	Oct	Nov	Feb	Mar
# collected	14	473	796	1267	249	47	1	63	305
% females									
P[1] 5+ yr	50.0	62.6	44.8	56.6	50.2	44.7		43.2	67.9
NP[1] 5+ yr	28.6	14.5	26.2	17.8	17.2	25.5		20.3	18.2
4 yr	7.1	6.8	9.7	9.6	8.0	14.9		1.6	0.3
3 yr	0.0	3.0	5.4	6.8	8.0	8.5		0.0	0.3
2 yr	0.0	0.0	0.4	2.2	6.4	4.3		15.9	4.0
1 yr	0.0	0.0	0.1	0.1	0.4	2.1		0.0	0.0
% males									
4+ yr	14.3	4.0	3.2	3.0	2.0	0.0		0.0	0.0
3 yr	0.0	6.4	7.1	1.2	1.2	0.0		0.0	0.7
2 yr	0.0	1.9	2.9	2.2	5.2	0.0		0.0	0.0
1 yr	0.0	0.2	0.1	0.2	0.8	0.0		19.1	8.6

[1]P = pregnant; NP = nonpregnant

[2]Percentages do not total 100 because pregnant females age 3-4 yr were omitted; see Methods.

Table 3. Percent pregnant for northern fur seal females age 5+ yr by month and region for samples containing 10+ females age 5+ yr during 1958-74.

Region	Month										
	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct
Pribilof Islands								91.2	84.8	85.6	
E Aleutian Islands							81.2	63.1	76.1	74.4	63.6
W Alaska							90.6				
W Gulf Alaska					84.6	81.4	70.5	20.0			
E Gulf Alaska			[1] 68.0	78.9[2]	89.7	77.6	47.2				
British Columbia				69.5	70.6	65.7	56.0				
Washington	75.0	71.6	71.7	70.6	70.3	64.8					
Oregon				75.0	75.3						
California		80.8	81.3	76.2	71.7	70.4	63.6				

[1]76.4 for 1950, as given in Taylor et al. (1955)
[2]75.6 for 1950, as given in Taylor et al. (1955) for 24 March to 1 April, 1950.

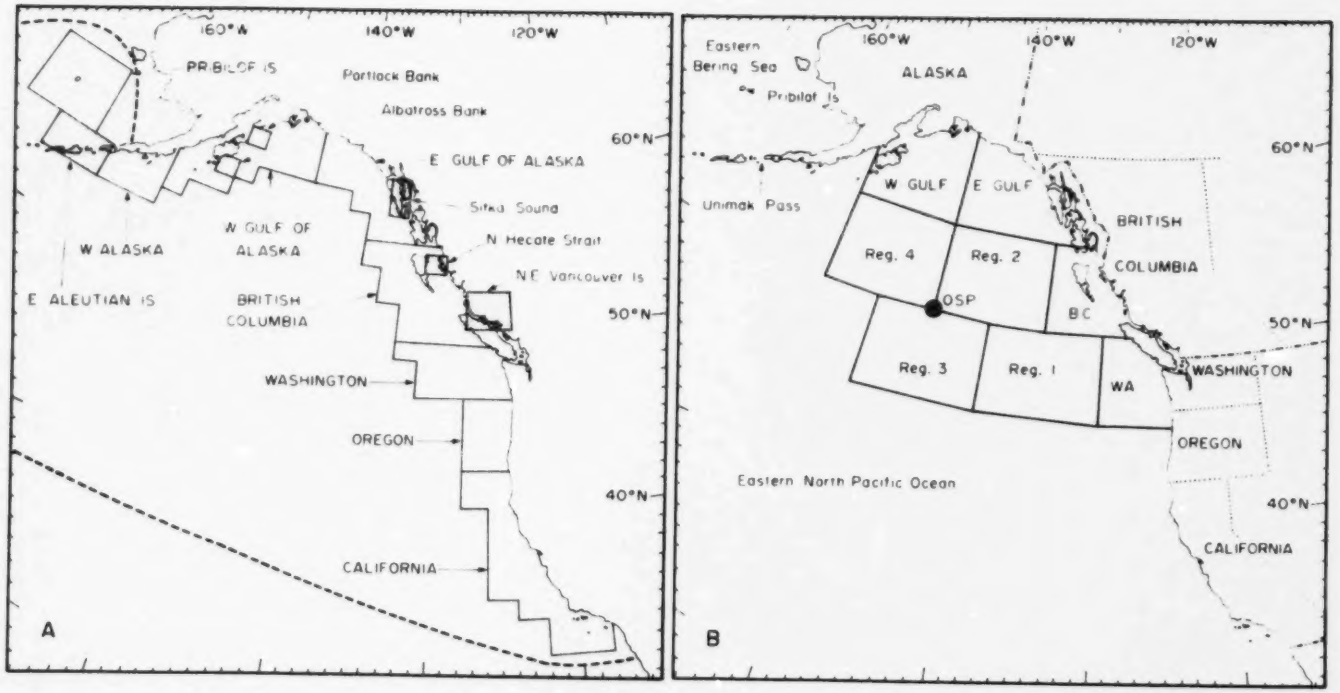

Fig. 1a-b. a) Geographic boundaries for the nine regions within the study area for data collected during 1958-74, the location of six sites (hatched) where some data were omitted from analyses and the geographic range of the northern fur seal off western North America (dashed line; from Kajimura 1980); b) Geographic location of place names used in the text and the geographic boundaries for eight regions used to examine sighting data collected by Manzer, Pike and MacAskie during 1956-77. OSP indicates the location of Ocean Station Papa.

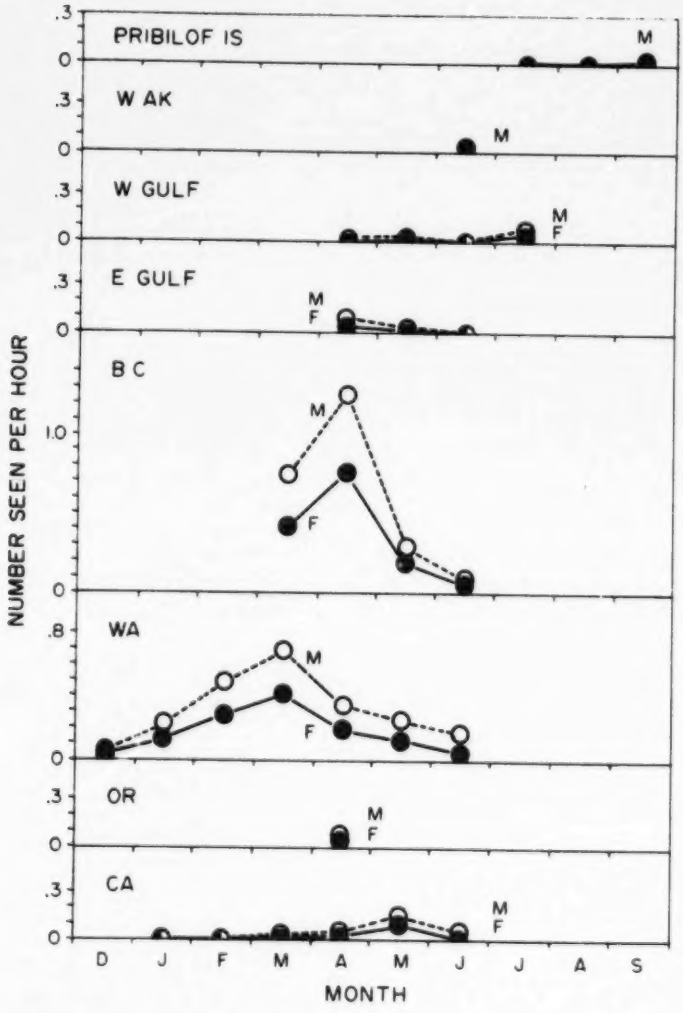

Fig. 2. Number of males (upper) and females (lower) age 1 yr seen hr^{-1} by month and region during 1958-74.

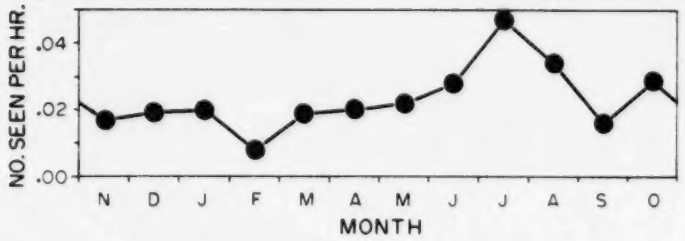

Fig. 3. Number of seals seen hr^{-1} by the crew aboard the Ocean Station Papa during 1960-77 based on data compiled by Manzer, Pike and MacAskie. Sample sizes given in Appendix Table 1.

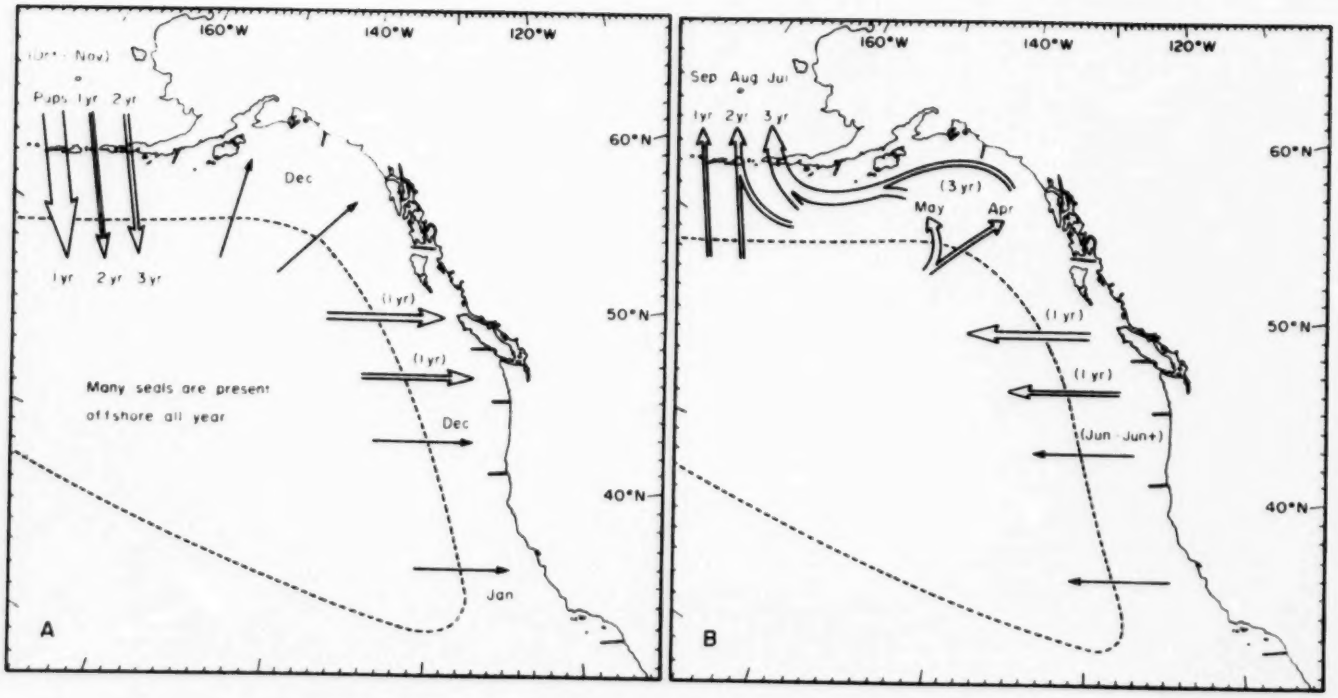

Fig. 4a-b. Schematic representation of the proposed route and timing for females age 1-2 yr and males age 1-3 yr when migrating from the Pribilof Islands to coastal wintering regions (a) and when migrating from coastal wintering regions to offshore regions and to the Pribilof Islands (b) Months in parentheses indicate departure times and months without parentheses indicate arrival times. Ages in parentheses indicate the main age group involved. Width of the routes indicate the suggested relative number of seals using the routes.

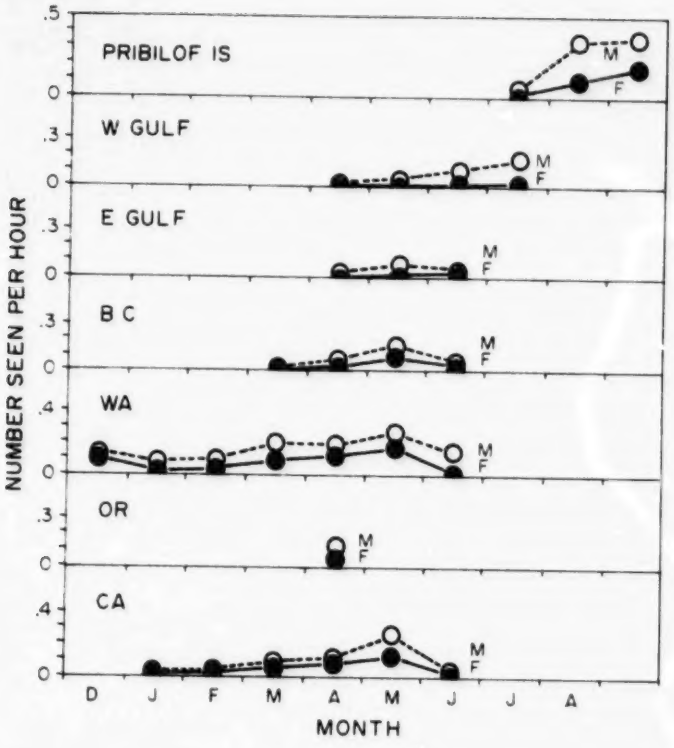

Fig. 5. Number of males (upper) and females (lower) age 2 yr seen hr^{-1} by month and region during 1958-74.

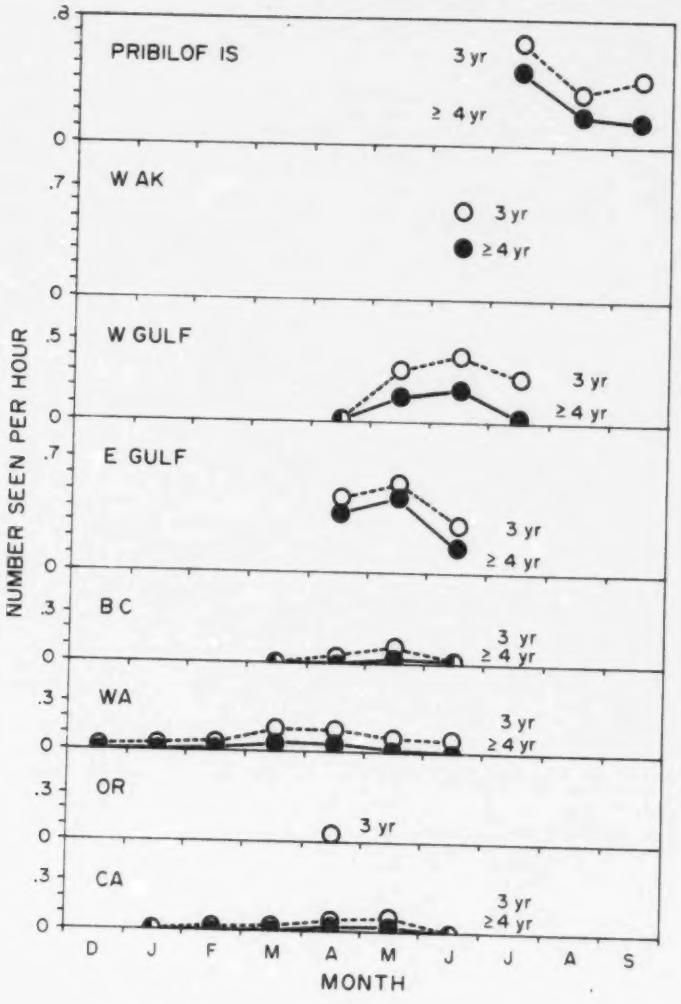

Fig. 6. Number of males age 3 yr (upper) and age 4+ yr (lower) seen hr^{-1} by month and region during 1958-74.

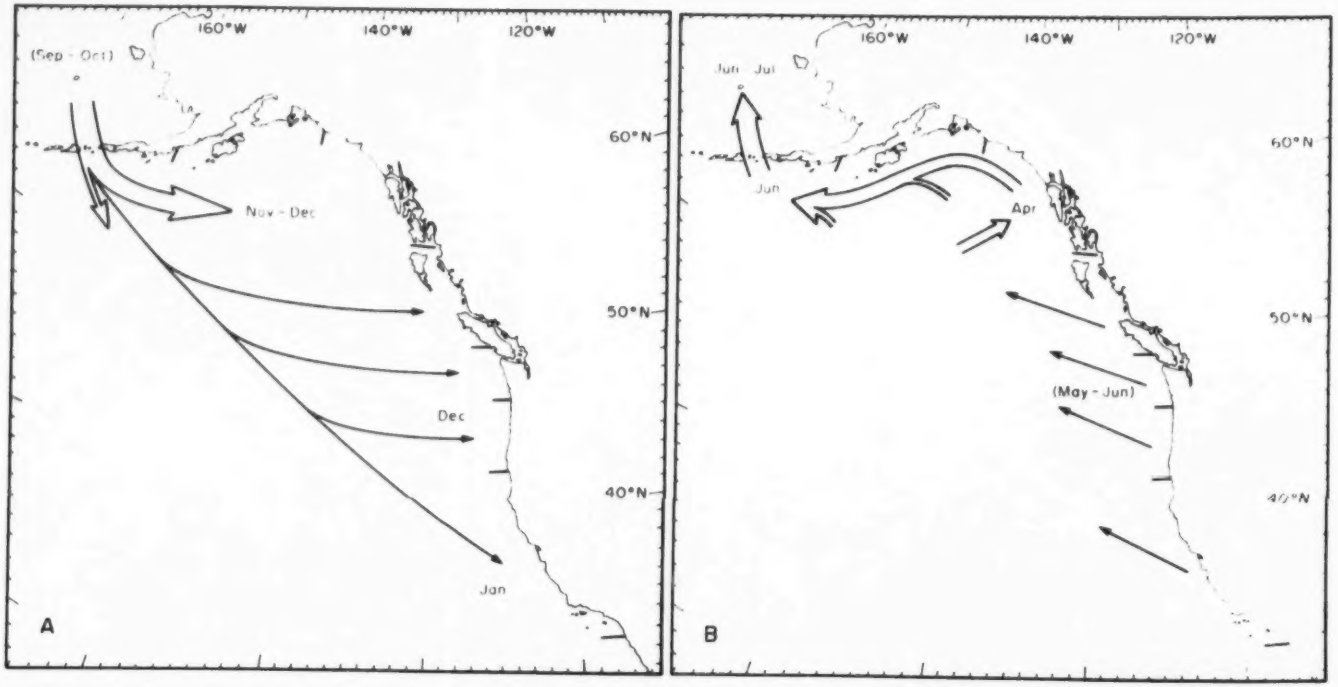

Fig. 7a-b. Schematic representation of the proposed route and timing of migration for males age 4+ yr when migrating from the Pribilof Islands to wintering regions (a) and from wintering regions to the Pribilof Islands (b) Months in parentheses indicate departure times and months without parentheses indicate arrival times. Width of the routes indicate the suggested relative number of seals using the routes.

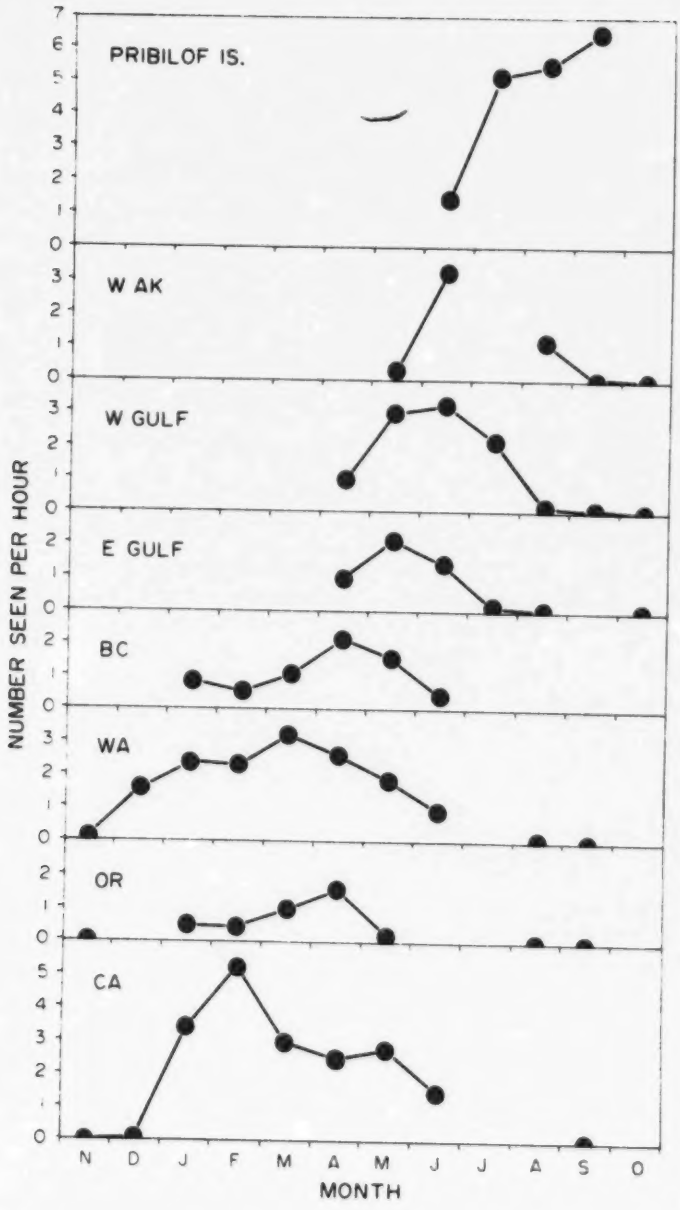

Fig. 8. Total number of seals seen hr^{-1} by month and region based on data collected during 1958-74. Note that the vertical scale differs from Figures 2, 5, 6, 11 and 13, but not from Figure 12. Samples sizes given in Appendix Table 1.

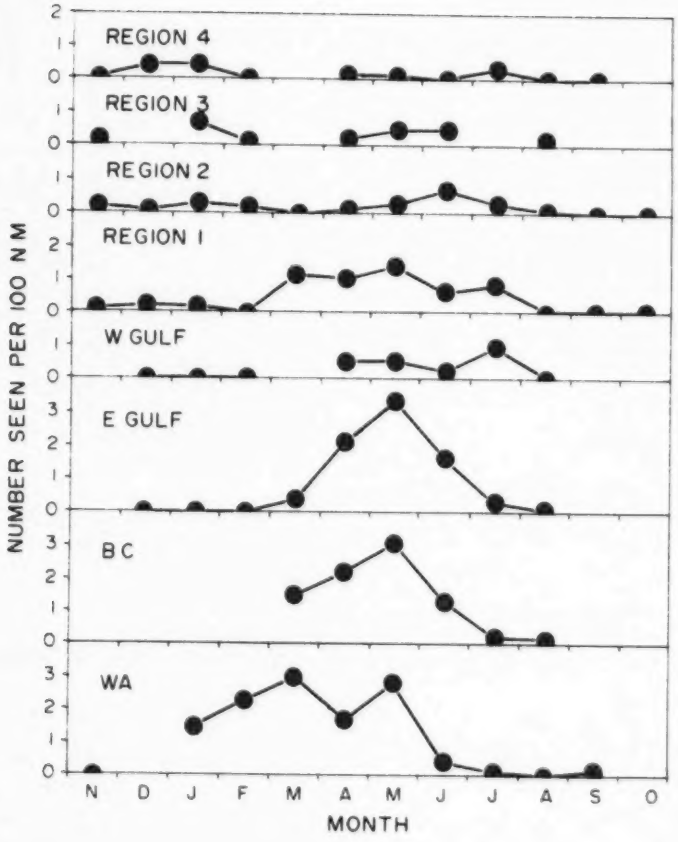

Fig. 9. Total number of seals seen 100 nmi $^{-1}$ (185 km) by month and region (Fig. 2) during 1956-66 based on data compiled by Manzer, Pike and MacAskie. Sample sizes given Appendix Table 1.

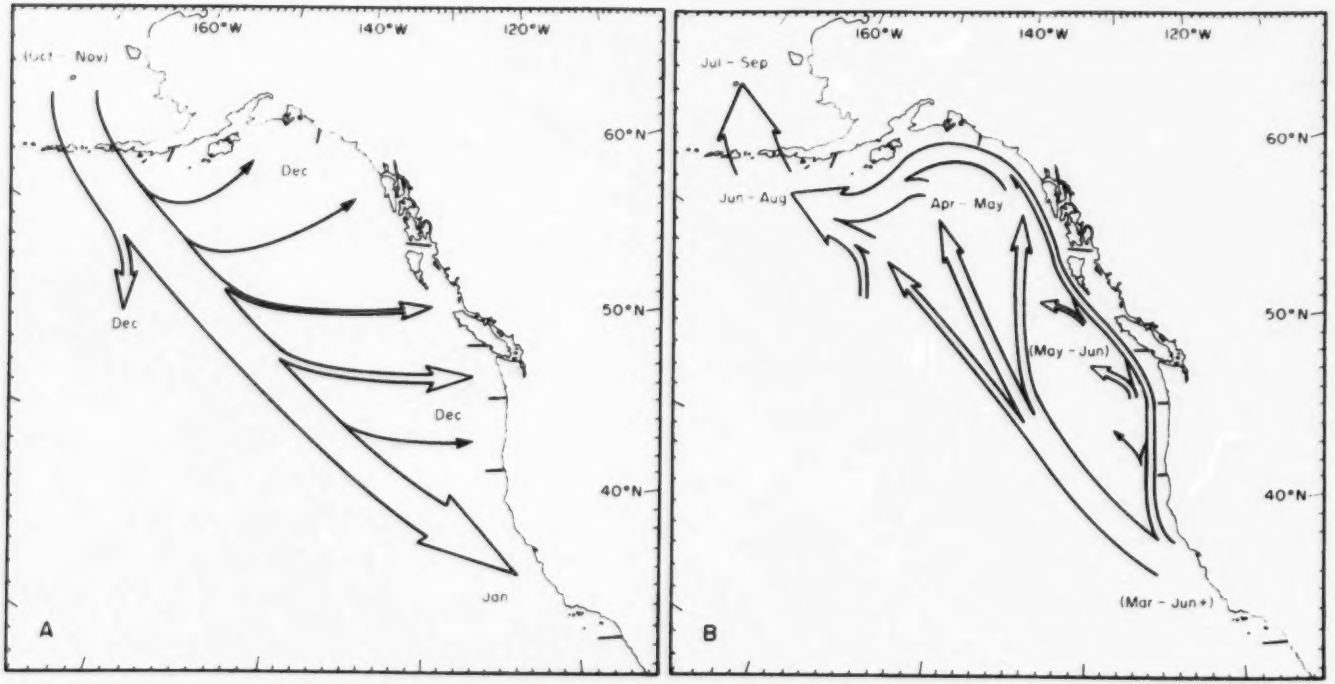

Fig. 10a-b. Schematic representation of the proposed route and timing of migration for females 3+ yr of age when migrating from the Pribilof Islands to wintering regions (a) and when migrating from wintering regions to the Pribilof Islands (b) Months in parentheses indicate departure times and months without parentheses indicate arrival times. Width of the routes indicate the suggested relative number of seals using the routes.

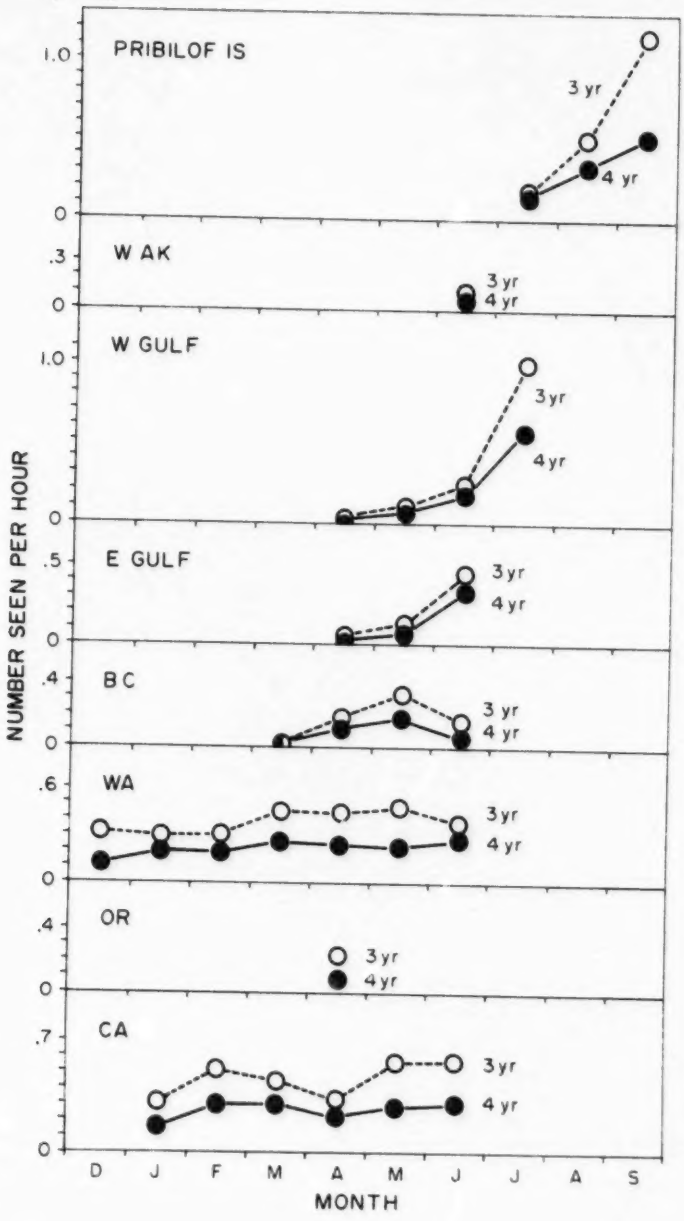

Fig. 11. Number of nonpregnant females age 3 yr (upper) and age 4 yr (lower) seen hr^{-1} by month and region during 1958-74.

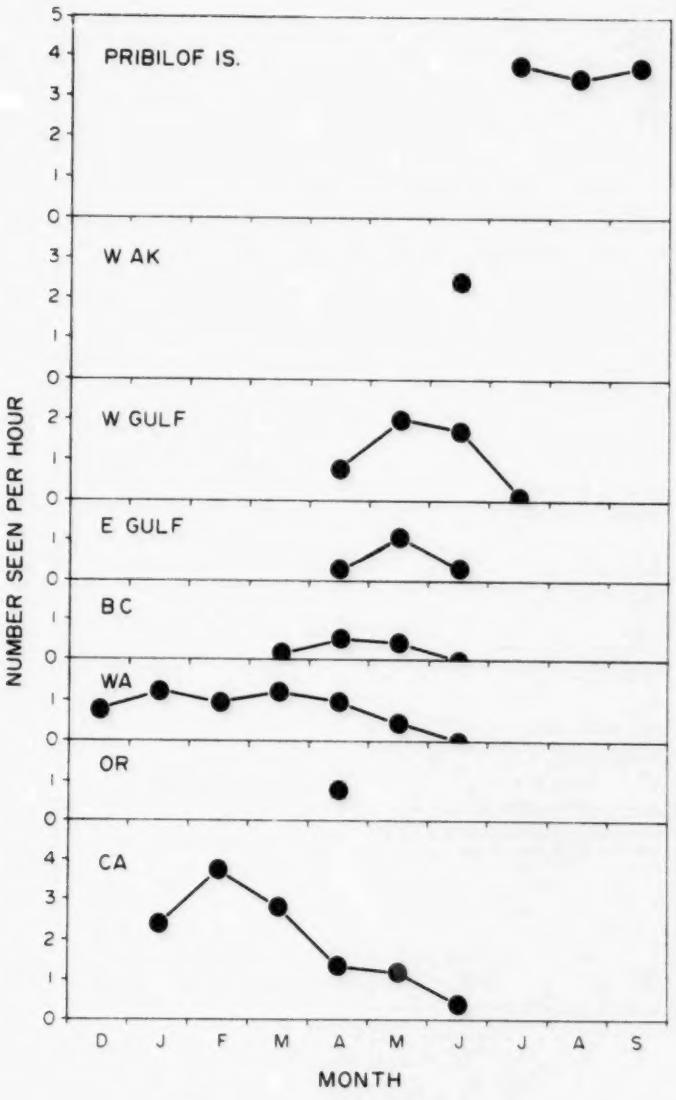

Fig. 12. Number of pregnant females age 5+ yr seen hr^{-1} by month and region during 1958-74.

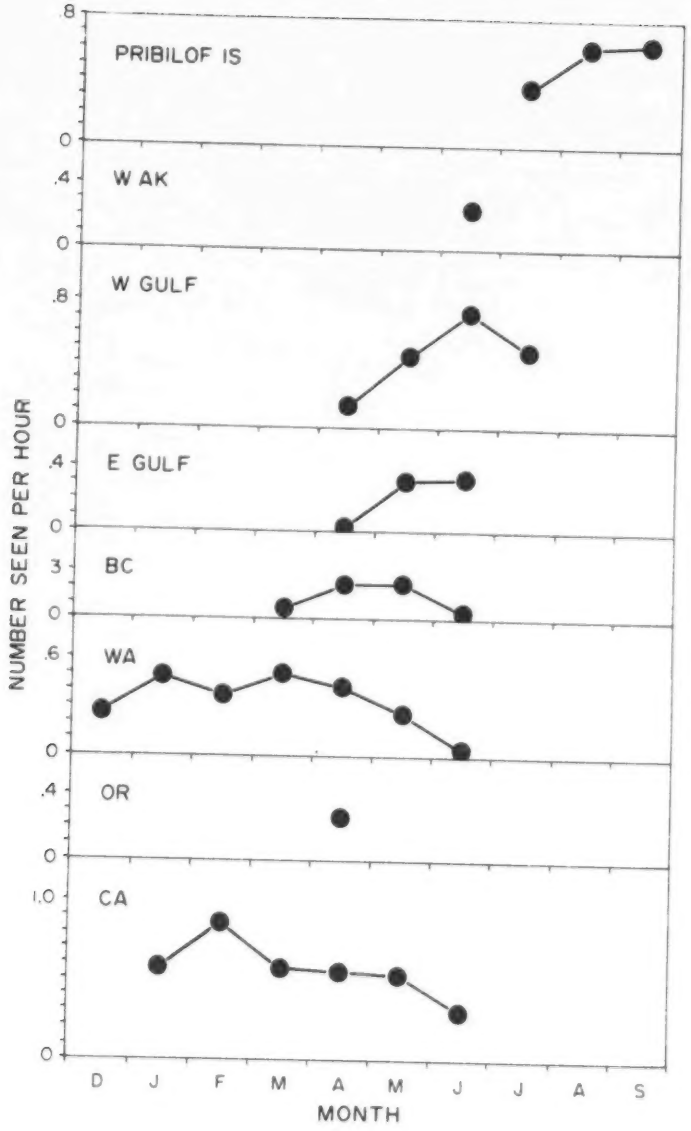

Fig. 13. Number of nonpregnant females age 5+ yr seen hr^{-1} by month and region during 1958-74.

Appendix Table 1. Sample sizes for Figures 2-4.

		Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct
Figure 2													
Pribilof I	# hrs	4	8						93	739	974	213	
	# coll.	0	0						3	793	1180	302	
W Alaska	# hrs							44	302	3	31	20	12
	# coll.							8	295	0	0	0	0
W Gulf	# hrs						98	698	372	84	72	10	28
	# coll.						264	1030	724	88	0	0	0
E Gulf	# hrs						345	131	102	21	12		17
	# coll.						82	75	85	4	1		0
BC [1]	# hrs		3	72	77	153	114	567	479	1	8		
	# coll.		1	21	155	62	97	327	91	2	0		
WA	# hrs	73	202	776	695	1319	2433	1430	122		71	23	
	# coll.	3	116	482	444	1263	2102	1126	49		0	0	
Oregon	# hr	10		39	33	77	240	36			65	62	
	# coll.	0		5	0	20	140	3			0	0	
California	# hr	26	95	540	1209	1046	505	394	154			49	
	# coll.	0	3	598	1412	818	346	340	96			0	
Figure 4	# hrs	1899	1656	1422	1550	2868	2856	4380	6080	6880	5026	2868	2740
Figure 9													
Reg. 4	# nmi	430	500	1660	660		4360	4720	3300	2050	1770	470	
Reg. 3	# nmi	600		760	920		3320	4340	2240		1070		
Reg. 2	# nmi	460	400	1730	570	340	3590	4045	4460	5260	4000	1300	780
Reg. 1	# nmi	1210	400	2670	1280	2700	6450	6985	4900	480	3300	1070	400
W Gulf	# nmi		360	620	1230		2380	4310	2020	1330	1920		
E Gulf	# nmi		400	360	490	940	1620	1890	2570	2740	2360		
BC	# nmi		394	890		1230	2650	3100	4600	2800	4200		
WA	# nmi	820		2840	1130	3890	4240	4400	7600	900	2950	1040	

[1]121 seals collected off northeastern Vancouver Island and 130 in northern Hecate Strait were omitted; see Methods.